Mate Choices in Animals and Humans. Individual Satisfactions and Social Behaviors

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Among animals and humans, the desires and satisfactions felt by individual members of a species drive reproduction and social life. Reproduction leads them to obtain partners and procreate, and social life leads them to ensure themselves a status and to exercise power. The activities carried out during reproduction fit not only into the framework of maintaining customary social organization, but also into that of its transgression. Relationships related to sex may be stable or ephemeral, organized or fortuitous, ritualized or brief; those that are connected to power may be based on hierarchized organizations, or the monopolization of space and its reserves, even its property in the case of humans. Observation demonstrates that among both humans and animals, infinite plurality comes from union, combination, and disjunction in these various modes.

During reproductive activities, sexual desire leads individuals to seek pleasure that will stimulate their brain's reward systems. The result is that the sensations felt cause individuals to perceive the other as a desirable source of satisfaction. This leads individuals to become attracted to, even to become attached to, one or multiple sexual partners. Among some species, including humans, the transmission of life is accompanied by parental behaviors of feeding and protecting the young. The satisfaction procured by power leads individuals to establish hierarchical relationships or even to divide up space. The desirable statuses thus possessed give prerogatives to those who hold them, but they are also the subject of continual reassessments. To mitigate these conflicts, individuals may then establish means of cooperation, and they may forge alliances that provide them with the satisfactions ensured by relationships and security.

It is known that the transmission of social status occurs among primates such as macaques and chimpanzees: a youth benefits from the privileged status its mother had if she possessed a high rank (Pereira 1995; Pusey et al. 1997; Kutsukake 2000). This is an example of a "social perpetuation" process, which we will discuss in more depth regarding humans below. Among humans, this tendency may make the forebears determined to choose a spouse for their descendants. This appears, on a level that might be described as ultimate—to borrow a term from evolution—as the chance to see the status of an individual or a clan continue in the next generation. However, if we take a proximate perspective, we will think of these human tendencies as the way for the forebears to experience the satisfaction of continuing in their status, even if this event is only in the realm of representations, aspirations, or fantasies. Whether the choices of the forebears please the descendants is another story; the descendants will have many ways to avoid and bypass the practices and other rules of marriage, a situation that is attested to by extramarital couplings and children born of these loves.

The purpose of this article is to demonstrate—convincingly, we hope—that similar principles among animals and humans demonstrate what generates the majority of modes and dynamics of mate choices. Thus from our perspective, it is not trivial to wish to connect and compare what is often perceived as arising from the course of nature in the case of animals and the course of culture in the case of humans.

Mate Choices in Animals

In order to perpetuate their species, animals use sexual reproduction, which combines the genetic material of the ova and sperm. At each generation, the individuals thus produced are only temporary structures doomed to disappear despite the means they have to preserve and lead a life of relationships. These individuals will give way to a new generation that comes from the reproduction of so me of their members. Among vertebrates, including many species of birds and mammals, this new generation often receives parental care. The young learn to develop behaviors and representations of their environment and their peers, they learn how to recognize particular places and individuals, and they gain the ability to feel emotions and have attachments-these are all acquisitions that permit them to have a complex social life. The time invested to choose and become attached to partners, to reproduce, and to raise their young accounts for a substantial portion of their activities. At the same time, it is not surprising to see that the body of work by ethologists on reproductive and parental processes is so extensive. Whether this research is the work of the objectivist school of Lorenz (1958) and Tinbergen (1951), or the behavioral ecology of Krebs and Davis (1978), all these studies seek to validate the theoretical and conceptual bodies of evidence by drawing largely on data from studies on reproduction and parental behavior. Using decoys, the objectivists have made extensive studies of coupling and feeding rituals.

Behavioral ecology, on the other hand, has studied different types of sexual, reproductive, and child-rearing strategies simultaneously founded on the Darwinian theory of sexual selection, and on later theories which considered that individuals optimize their behaviors in order to gain benefits and minimize costs. We will summarize these theoretical foundations and conceptions as follows. Within sexual species, the creation of a new generation of individuals is constrained by mate choices and partner choices of the parents in the preceding generation. Darwin (1859; 1871) had already imagined that natural selection alone was not enough to explain the evolution of species. He had suggested, despite the reticence of a number of his colleagues, who nevertheless were receptive to his theories, that there existed a process of "sexual selection." Sexual selection postulates that partner choice will be constrained not only by the preferences that the females will have for some types of males, but also by the competitions the males will enter into in order to be in a favorable position to choose or be chosen by the females. The theory of sexual selection has spurred many debates. It is known that Wallace (Slotten 2004), the codiscoverer (or coinventor) of the theory of natural selection, did not agree with Darwin on this point. However, toward the end of the twentieth century, many authors adopted it.

Behavioral ecology brought new tools of analysis and interpretation, often borrowing from the social or economic sciences. Many studies utilized the notion of behavior optimization. For example, it is possible to see that an animal devotes itself to one or another activity in order to minimize costs and maximize benefits. It is therefore useful to understand the animal as an agent that manages a "time-energy" budget in order to best guide its chances to survive and reproduce. It follows that the various actors in this social life, the individuals, may have

convergent or divergent interests. For example, in reproductive structures in which the females expend more time and energy than the males on raising the young, the females will have more to lose than the males from a reproductive failure. Indeed, in any "affair," the individual that invests more is the one that has the most to lose if the affair fails. Ethologists therefore predict that females will be more selective and attentive to the choice of their partners than males. As Darwin foresaw, they choose the males more than the males choose them. One may also consider, in another form, that during reproduction there are more available spermatozoa than ova, so the ova constitute a rare resource. Thus females have fewer reproductive "tickets" than males do, and every time they use one, they cannot waste it as much as the males can waste theirs. They therefore need to be attentive so as to best optimize the ticket's use.

Even if one observes results leaning toward the hypotheses formulated above, many authors doubt that individual members of a species will have the mental abilities to carry out reasoning that would lead to such decisions. Because it is improbable that the animal perceives (deep down) the basis for this reasoning, one should instead imagine that its interest in a mate is moved in this direction by its neuroendocrine functioning, which is the product of the long phylogeny of its species. The wirings and processes selected by evolution between inputs and outputs, that is, the perception-cognition-emotion-action chain, would perform the work. The social behaviors of the animal and the strategies it deploys during its life of relationships are from this point of view the "ultimate causes" that transcend individuals' mental lives. Just as a rock does not need to fall in order to learn about the laws of gravity, an animal does not need to perceive the interest of optimizing its activities in order to nevertheless engage in behaviors that achieve this goal and make it an *economicus* agent. The phylogenetic laws to which evolution subjugates the animal remain unknown to it even if it puts them into practice.

Pragmatic Models of Partner Choice

The models that ethologists use to "explain" partner choices can for the most part be categorized as what we will call models of "pragmatic choices," that is, choices that present a certain utility with regard to reproductive efficiency; the more popular models are based on the Darwinian theory of sexual selection. The pragmatic models can be divided into three major groups.

A first set of models believes that females constitute the main agent of choice and that all the females of a same species have basically similar models of the ideal partner. For example, he would have superior genes, enjoy good health thanks to a sound immune system, and have exceptional longevity. Of course, all these pieces of information are not necessarily accessible at the moment of mate choice, and the choice will be made based on the perception of indicators that are correlated to these attributes. A beautiful mane, high hierarchical status, or longer and more colorful feathers will often be reliable indicators—honest signals—that will enable a female to identify the coveted partner or be stimulated by him.

Among birds, and more specifically the canary, *Serinus canaria*, we were able to show that the females all preferred a particular structure of male song known as *sequence A* (Vallet and Kreutzer 1995). This song phrase has the particularity of being difficult to sing because it requires a close coordination of the right and left bronchial tubes, and the syrinx, which is the vocal organ in birds (Suthers et al. 2004). In addition, the two cerebral hemispheres involved

in song production must coordinate their activities (Halle et al. 2003). "Superstimuli" may even be synthesized and may produce attractions that are higher than those of natural signals (Draganoiu et al. 2002). These motor performances can be compared to the work of a juggler, who would coordinate very quickly and asynchronously his right and left hands. This sequence A has also turned out to be a good indicator of males' hierarchical status (Parisot et al. 2004).

Other arguments can be made for pragmatic partner choices, namely, that it is important for females and males to choose partners that are not related to them, that is, genetically distant enough to avoid the risks that consanguineous pairings would carry. In this case, the best partners or the partners to avoid generally differ from one individual to another because most individuals do not have the same relatives. The models of partner choice regarding this scenario therefore vary according to the individuals, and not all females would share attractions for the same males.

According to a third perspective, over the course of their lives, individuals would have the advantage of modifying their model of partners based on reproductive successes or failures experienced with previous partners. Hence, the models vary not only from one individual to another, but also over the course of an individual's life (Kreutzer 2002). In the case of canaries, we have been able to show that females modify the value they accord to the songs of former partners. Reproductive successes reinforce this value while failures make these songs less attractive (Béguin et al. 1998).

Aesthetic Partner Choices

Are all the possible models of partner choice exhausted by these pragmatic approaches? On numerous occasions Darwin defended the theory that there exist aesthetic choices (Hoquet 2009)¹. Some authors continue to take up this suggestion, and they experiment to prove its legitimacy. We share their approach, and this point of view will be useful for the theory we are defending, namely that the search for pleasure and the desirability of aesthetic stimulations accompany the search for a partner (Kreutzer 2001). Establishing whether such choices are in synergy with the search for a long-term optimal adaptation (as the pragmatic models formulate it) would demonstrate the stabilization of the criteria of choice.

We can broach the topic of aesthetic choices by revisiting Darwin (1871, 1874)². He invites the reader to extend to animals the abilities seen in humans and often attributed solely to them: "Man and many of the lower animals are alike pleased by the same colours, graceful shading and forms, and the same sounds" (page 93); "The senses of man and of the lower animals seem to be so constituted that brilliant colours and certain forms, as well as harmonious and rhythmical sounds, give pleasure and are called beautiful" (page 584). Darwin also invites the reader to see in this tendency toward aesthetic taste an ability of the nervous system:

¹ As Thierry Hoquet notes in his analysis of Darwin's work: "If beauty is of no 'use' for the individual, then it remains unexplained by natural selection" (2009, 222); "sexual selection extends the domain of the useful to the set of characteristics that are judged beautiful" (2009, 223).

² Note that the content refers to *The Descent of Man and Selection in Relation to Sex*, 1st ed. (1871). However, here the 2nd ed. (1874), was the source for all the citations. Texts from "<u>http://darwin-online.org.uk/</u>"

Everyone who admits the principle of evolution, and yet feels great difficulty in admitting that female mammals, birds, reptiles, and fish, could have acquired the high taste implied by the beauty of the males, and which generally coincides with our own standard, should reflect that the nerve-cells of the brain in the highest as well as in the lowest members of the Vertebrate series, are derived from those of the common progenitor of this great Kingdom. For we can thus see how it has come to pass that certain mental faculties, in various and widely distinct groups of animals, have been developed in nearly the same manner and to nearly the same degree. ... He who admits the principle of sexual selection will be led to the remarkable conclusion that the nervous system not only regulates most of the existing functions of the body, but has indirectly influenced the progressive development of various bodily structures and of certain mental qualities. ... musical organs, both vocal and instrumental, bright colours and ornamental appendages, have all been indirectly gained by the one sex or the other, through the exertion of choice, the influence of love and jealousy, and the appreciation of the beautiful in sound, colour or form; and these powers of the mind manifestly depend on the development of the brain (Darwin 1874, 616-17).

Darwin frequently uses birds as an example to explain his remarks, as in this case: "When we behold a male bird elaborately displaying his graceful plumes or splendid colours before the female, whilst other birds, not thus decorated, make no such display, it is impossible to doubt that she admires the beauty of her male partner" (Darwin 1874, 92). And he concludes from this "that the pairing of birds is not left to chance; but that those males, which are best able by their various charms to please or excite the female, are under ordinary circumstances accepted" (Darwin 1874, 422).

Aesthetic Choices and Reward Circuits

How can we today objectify these aesthetic choices that Darwin presents? We postulate that they are carried out by the females when they manifest emotions and accept as partners males whose splendors, vocalizations, and behaviors are more stimulating for them than those produced by other males. Of course we know that females prefer males whose symmetry and vivid colors could be indicators of their quality (Møller 1992; Anderson 1994). Do these results together exhaust the question of "aesthetics"? In the cases of humans and animals, it is known that certain signals are more exciting than others and stimulate certain nerve centers that cause a feeling of pleasure. The individual giving off such signals can subsequently exploit the receiver and influence the receiver's choices. For males, the important thing (to gain the best advantage) would be to stimulate the females so that they interpret the source of the pleasure as aesthetic. The theories of "sexy son" (Weatherhead and Robertson 1979) and "sensory exploitation" (Ryan 1990) are good candidates for advancing in this direction. These theories show how the morphology and behavior of a male emitter can be used to exploit a perceptive predisposition that already exists among the receiving females. In addition, in the case of sensory exploitation, the authors demonstrate that in the course of evolution it is not necessary for the females' sensory and perceptive predisposition to lead them to male partners that would be of better quality; what counts is the power to stimulate the females (Burley and Symanski 1998).

Aesthetic choices and the ability to feel pleasure from beauty are Darwinian preoccupations that today have regained a topicality. Researchers have recently shown that animal brains have reward circuits that are activated in the presence of certain social events, for example, those that involve choosing partners (Aragona et al. 2003), or song production in the case of

birds (Hara et al. 2007). When animals produce, see, or hear certain behaviors, this can stimulate their reward systems (Ikemoto and Panksepp 1999). For animals, social life is accompanied by encounters that are more or less pleasing, and the presence of one individual rather than another will bring them more or less satisfaction. These facts go far beyond the simple encounter of "exciting" objects, the superstimuli that the objectivists studied in the mid-twentieth century.

Today it is undeniable that animals feel pleasure, and that this enables them to establish and maintain ties with certain equals. As behaviorism states it, animals seek and repeat what is pleasant to them. What they feel is a driving force of their motivation to act. At this stage, it is tempting to imagine that pleasure and reward circuits give particular values to some signals, individuals, objects, and situations. This enables mental representations based on these attractors, which can be used to form cognitive categories. During evolution, what appears pleasant must have served as a basis to construct the subjective categories of "beauty" and "good." Even before the emergence of a linguistic labeling, such a conceptualization must be possible.

A major interest of this work lies in the fact that it allows us to objectify the subjectivity of animals. It is possible to pass from behavior to the study of mental life; ethology and animal psychology, two disciplines that have often worked separately, can finally meet. However, any system incurs risk, the main one being that of having the faults of its attributes. And we know that the reward and pleasure circuits are also those that can be perverted, and can lead to addictions and dependencies (Kelley and Berridge 2002). Animals, like humans, use the same reward and pleasure circuits, which appeared very early in evolution. They can succumb to the pleasure of desiring an object for the stimulations they gain, and not for the object's utility. Some authors even compare the stimulations of social life to addictions (Insel 2003). The quest for pleasure alone leads to pleasure for pleasure's sake, and its absence causes frustrations. From this perspective, the search for power for power's sake can derive from the pleasure felt from possessing for possessing's sake, and not for preserving and transmitting. This quest is accompanied by a risk, that of seeking to constrain and subjugate the other, not only to better possess and control, but also for the enjoyment and satisfaction that this secures.

The Particularities of Sexual Selection in Humans

Among humans, the desire to self-perpetuate passes through transmission, as well as the real and imaginary control of their status through their lineage. It follows that during human evolution, aesthetic choices and the rules for choosing mates became disconnected. Indeed, how would one generation leave to its successors the task and freedom to choose its partners? The stakes would be too high to leave to the following generation the freedom to choose. Control over the next generation becomes necessary, and it is realized by imposing on it the rules of mate choice. But the following generation finds a margin of freedom to produce descendants through bypassing the rules by, for example, having extramarital relationships or marriages outside the norm, or without the consent of the forebears, not to mention fortuitous reproductions within ephemeral contexts or as the fruit of furtive copulations. We will develop these points now. Let us return briefly to the two methods of selection that Darwin used to demonstrate evolution. He asserted that along with natural selection proper, another force is at work, a force he named "sexual selection." Natural selection seemed to him to act on the "variations" between individuals to further those that contribute to adaptation in given circumstances, and would therefore enable the individual to survive and reproduce. Sexual selection was then perceived as the mechanism by which the surviving individuals reproduce variations; it rested on what Darwin named "the law of battle," that is, competition between the males for possession of the females, and the subsequent choice made by the females from among the dominant males. Moreover, Darwin believed that sexual selection was independent of natural selection. According to him, it was responsible for sexual dimorphism, which was likely to result in male phenotypes that would handicap survival, such as birds whose exuberant plumage is an obstacle to flying or a signal to predators, or stags' antlers, which are a hindrance for passing through dense forests. A sort of evolutionary pendulum seemed to be at work, placing a limit on the modifications that compromise survival.

Darwin also thought that sexual selection must have been applied to humans at the very beginning of their history, but had thereafter subsided due to the development of a culture that, through complex matrimonial institutions, tended to alter, even minimize, the purely physical aspects of desirability and replace them with other, cultural, ones. Therein lies the problem posed by sexual selection, which can be formulated as follows: should relations between men and women, and particularly matrimonial relations, be interpreted as the pure product of exclusively cultural or social determinants, or would it instead be appropriate to imagine that other factors, which are unconscious because they are of a biological nature, also play a role? This also leads to a questioning of the relations between different types of causes, proximate and ultimate. Some evolutionary perspectives imagine that the social and cultural factors of marriage are only measures taken by the figures situated at the top of the hierarchy in order to reproduce more than the others, the ultimate cause thus being reproductive success. Here one can recognize the so-called skew theory, which maintains that in hierarchical societies (and nearly all societies are hierarchical, as soon as one leaves the category of the hunter-gatherers), the individuals located at the summit of the hierarchy use their better access to resources to reproduce more. Position in the hierarchy and reproductive success would thus be linked³. If this theory were exact, then the top categories would manipulate all the elements of choice in order to promote their own reproduction. However, we believe that here there is a confusion between reproduction and perpetuation. What the upper strata of the hierarchy transmit are the means of their domination (economic, status, or other), by which they ensure their domination⁴. The more complex the society, and the more that privileged access to resources comprises non-dietary elements, the less these elements are connected to purely reproductive success. The argument defended here is that as soon as one reaches a level of the hierarchy where privileged access to resources is no longer purely dietary, social perpetuation is distinct from biological reproduction; hence, there is no reason why those who are best provided for should leave substantially more descendants than the others.

Contrary to what skew theory maintains, we will argue here that biological reproduction and social perpetuation are independent of each other, and that herein lies a particularity of human beings. This amounts to saying that the choice of partner may be dictated by inheritance or aesthetic considerations, or even by biological ones (or more likely by a combination of these factors), but that they are not mutually exclusive.

³ For a summary of these theories, see Kyle Summers (2005), 106–35.

⁴ This is not necessarily seen as illegitimate and therefore does not fall automatically into the Weberian category of power, as is believed by L. Betzig (who, not knowing about Weberian sociology, prefers to call any form of power "despotism").

Reproduction and Perpetuation

So as to clarify the debate, here we propose to distinguish what falls under "biological reproduction" (having descendants)—which necessarily has a very long history—from what introduces the prestige on which "social perpetuation" (having successors) depends, and which does not predate the appearance of social hierarchies. In other words, the essential particularity of sexual selection in humans would come from the fact that it connects two mechanisms. One mechanism was established at the dawn of human history and is based on the anticipation of good reproductive qualities in others, particularly through the feeling of physical beauty. The other mechanism—the role of domination—has a past that is just as long, but this has been strongly reworked by culture over the course of human history. Human history would have altered the anticipation of fertility by adorning it with charm and desirability, while it would have completely reconstructed domination by stripping it generally of any physical dimension in order to make it purely social (mainly through inheritance). Both mechanisms are linked to reward systems, and these systems may therefore take precedence; this all the more so because, according to our hypothesis, they are independent.

Sexual Selection: The Culturalist Hypothesis

The theory of kinship, which constitutes the backbone of nineteenth-century anthropology, is based essentially on the idea that in traditional societies, marriage is constrained by rules of alliance that aim to perpetuate social entities (lineages or local groups). From this perspective, it follows that the matrimonial union is essentially, if not exclusively, a social matter; it owes almost nothing to the sentimental inclinations of the interested parties, in other words, it owes nothing to desire. If this were truly the case, the forms of partner choice in human beings would not pertain to sexual selection in the Darwinian sense of the term because the reproductive qualities of the relevant parties would not be in question. The forms of partner choice would pertain solely to the perpetuation of a social position or a legacy. This conclusion, which much of the anthropological literature invites the reader to arrive at, is nevertheless up for discussion. One may even find arguments to dispute it in ethnographic relations that seemed, during the twentieth century, to justify it. Hence, the ethnography of Australian aboriginal people, which served as the main basis for theories suggesting that marriage was a solely "social" act (because the marriages were subjected to "strict" rules based on the exchange of sisters according to repetitive mechanisms independent of the will of the actors), nonetheless displays paradoxical aspects. Spencer and Gillen (1899) offer one of the first descriptions of this, referring to a rule of obligatory marriage among the Arunta people, but also three other matrimonial procedures that were just as common: seduction by magic, pure and simple kidnapping, and removal suggested by a discontented wife. How can one not see the effect of desire in this case? It is quite clear that all types of distortions insinuate themselves between affirmed principles and actual practices. However, it is precisely these distortions that are the basis of actual behaviors. It is truly a question of behaviors when one becomes interested in sexual selection. In any event, if the individuals do not blindly obey the rules of alliance or decisions of patrimonial interest, but have a certain autonomy in the matter of matrimonial or simply emotional choice, the Darwinian principle of sexual selection has every likelihood of being applied.

Sexual Selection: The Biological Hypothesis

It is easy to show that matrimonial choices entail considerations pertaining to what is here called "social perpetuation" (transmission of status or property). It is also relatively easy to show that these considerations to a certain extent contaminate the actors' aesthetic perceptions (the rich have more resources and incentives to mold themselves to the local criteria of desirability, which, furthermore, they contribute to defining). It is more difficult, but just as important, to show that these choices also draw on unconscious preferences that introduce an assessment—which is perceived not as such, but as a form of "beauty"—of the reproductive abilities of the individuals involved.

Several studies have aimed to show that behind preferences for varied female silhouettes (thus illustrating one conception of "beauty"), there are actually some hidden constants that are not at all arbitrary: the aesthetic choices would only privilege silhouettes that are more favorable than others for reproduction, which would thus have implications regarding natural selection (Marlowe et al. 2005). The fact that particular silhouettes are more favorable is the result of a certain combination of hormones that varies according to morphologies. In choosing a certain type of silhouette, men would also unknowingly be choosing reproductive qualities⁵. Whether or not the aesthetic choices conceal unconscious biological choices only confirms that these choices exist. Moreover, if they are not independent of reproductive qualities, then they are not only a cultural product; they are also deeply anchored in the history of humanity.

Reproduction and Perpetuation: The Combination of Two Forms of Desirability

In the case of human beings, sexual selection does not take into account only the partners' physical or behavioral desirability; it is also based on an assessment of the material advantages presented by this union, what is here called "social perpetuation" (Augustins

⁵ This research has been conducted in several stages. In a first phase, Marlowe and Westman (2001) showed drawings of front-view female silhouettes to two samples, one American and the other African (Hadza hunter-gatherers). The silhouettes differed in terms of the ratio between the waist and the hips. The lower the ratio, the smaller the waist compared to the hips ("wasp waist"); conversely, the larger the ratio, the less the silhouette was bent into a curve in the waist. A ratio of 0.7 seems to be the most pleasing to the American man; however, it so happens that this ratio is, from a physiological point of view, the one that seems to optimize the relationship between testosterone and estrogen, so as to also be the one that makes it possible to predict good reproductive abilities in the woman. The choice was slightly different among the Hadza hunter-gatherers, who favored a higher ratio (thus a less narrow waist), but this difference does not seem to be of a nature to call the reasoning into question insofar as, according to the authors of this study, this ratio corresponded to that of young women, that is, fertile women, in the society in question. Other researchers have argued that these studies were marred by ethnocentrism inasmuch as what they were measuring was not the aesthetic choice of the populations studied, but the American influence in the world, an influence that spreads its styles and preferences. They cited as proof the fact that a Central American population, far from such influences, did not make the same choices, and clearly favored high ratios (that is, stout women). The holders of the initial theory did not concede defeat; they suggested a new series of tests based on silhouettes viewed in profile and not frontally, such that the waist-to-hip ratio (WHR) appeared not as a ratio between the waist and the hips, but between the waist and the buttocks. Thus it is an issue of two measurements, both of which contribute to the WHR. The African men then favored low ratios (narrow waist compared to buttocks), while the Americans chose higher ratios (less-contrasting profiles). The authors concluded from this that preferences based on the actual shapes of women varied according to regions: where they have wide hips, it is a low ratio that is preferred, and where they have stout buttocks, it is also a low ratio that is preferred. The preferences would thus be directed toward the level that the presence of various hormones optimizes, all while favoring different shapes. It should be recognized that aesthetic preferences are, at least partially, connected to biological characteristics that are important for reproduction; the explanation for this is undoubtedly that they were put in place in a time period that is very distant from human history, in a period when each individual's reproductive abilities were totally decisive for the survival of groups.

1989). There are thus two types of proximate causes in matrimonial behaviors, which pertain to what may for some people be called "personal desirability" (where aesthetic preferences come into play), and for others "status desirability" (which involves property or social status advantages presented by each of the possible spouses). Together, these two proximate causes constitute a final single cause that may be defined as "sexual reproduction in the best possible material and social conditions." The desirable partner will therefore be the one who, based on each person's qualities and aspirations, maximizes the two forms of desirability. This amounts to saying that there necessarily exists two sets of parameters in matrimonial choice: personal (and these depend on physical or behavioral, thus on aesthetic, attraction) and social (and these bring in the attraction of material advantages).

Thus, any union, whether matrimonial or not (but all the more so if it is), involves considerations that are implicit in physical qualities as well as in aspects of the social position of the involved parties. These two types of qualities do not need to be consciously formulated, and may be joined in an overall conception of desirability; they are no less analytically distinct⁶.

Notwithstanding, the balancing of different types of qualities is not solely the jurisdiction of the individual; one may on the contrary think that their distribution is specific to the environment in which they develop. It is the case with societies in which some social milieus impose constraints on marriages such that the share of personal desirability has been nearly eliminated: the unions are thus obligated and negotiated by the parents without the agreement of the affected parties even being required. In other societies, it is clear that sexual selection has become mainly, if not exclusively, social: its sole target has become the perpetuation of status or $legacy^7$. On the contrary, these are cases in which only the desire aroused by a particular person seems to play a role, with hardly any consideration for the material aspects of the union. These two extreme cases constitute two deviations with regard to what one may think is the characteristic of human sexual selection that, by necessity, associates biological reproduction with social perpetuation. One of the two deviations refers to the oldest aspects of sexual selection (that which favors, through the physical, the anticipation of fertility; it is aesthetic); the other owes practically everything to culture (that which chooses social prestige as the fundamental criterion). Moreover, they can appear relatively lasting to the extent that they are associated with reward principles: some accumulate property or material advantages, and others accumulate romantic affairs. One may validly suppose that the more the transmission of status and inheritance of property are important in the course of life, the more the perpetuation aspect must take on importance (in other words, the more marriages are arranged without consideration for particular inclinations). This applies as much to the top of the hierarchy as to social positions that are closely associated with legacy. Once in place, these strategies seem to become kinds of behavior models associated with social groups on the point of anchoring themselves in myth: the "rich" of the nineteenth century married among themselves without worrying much about the charm of their wives, but they

⁶ Advertising obviously plays completely on the intermingling of categories, trying hard to present flattering figures from two points of view by combining the two.

⁷ Saint-Simon's two marriage attempts provide a good example of this. He himself said that in both cases, it was the alliance with the father-in-law that motivated him. Furthermore, he had never seen the girls whose hands he was seeking. In the first case, there were three sisters: the oldest (she was fourteen years old) was devoting herself to religion; the second was "deformed," and the last was only twelve years old, but Saint-Simon himself said that he would have adapted very well if the oldest were not available; the father did not want that. In the second case, there were two sisters whom he found equally pleasing when he met them; he ultimately married the second one, but he did not know her more than the other when he made the request to her father, the Marquis de Lorge. (This note was added at the suggestion of one of my reviewers. I express my gratitude here.)

impregnated their maids, while the poor of the same era united for love and drowned their misery in absinthe.

The fundamental problem that is posed to most human societies comes from the fact that enviable social positions are rare, and those who hold them wish to preserve them. This involves having a sufficient number of descendants to cope with the risks, but in a small enough quantity so as not to create a fatal competition. These two requirements are obviously contradictory. A frequently encountered solution, at least in the Western world, is primogeniture, which leaves perpetuation, and to a certain extent reproduction, to a single child. It is all the more "profitable" as one is high on the social ladder, enabling the perpetuation of one's status to the detriment of younger children, all the while multiplying one's descendants as much through the legitimate process as through the alternative. For example, one notable study showed that within the sixteenth-century Portuguese nobility, the highest stratum married its eldest sons preferentially to well-endowed daughters of the gentry (for which the sons had no chance for social success other than by attaching themselves to perilous overseas military expeditions), while the daughters of the nobility became nuns (Boone 1986). In a very similar order of thinking, the court nobility under Louis XIV entered into its marriages for reasons of maintaining status, without consideration for any possible inclination of the future spouses; there resulted, as Saint-Simon shows, a world in which extramarital liaisons were numerous and almost public knowledge.

One may therefore think that the more the social position occupied at a given moment rests on a foundation of status or a transmissible legacy, the more the social perpetuation aspect will play an essential role in marriages (the more the "reproduction" aspect that is based on desire aroused by the physical and emotional risks being neglected). Furthermore, any non-servile social position may be materially and symbolically gratifying if it is upheld as honorable in the society under consideration: it therefore has its principle of reward. A matrimonial strategy based on the homogamy of social milieu or status is therefore likely to strengthen this principle of reward. However, personal, emotional, and sexual attraction is another principle of reward that is just as powerful, if not more so. One may consequently suppose that compromises between the two principles of reward are established, and that perpetuation and reproduction compete equally.

What Demography Says

Demographers' research on homogamy is considerable, and some is already quite old; it consists in measuring, in a given population, the proportion of marriages entered into by people who resemble one another according to a given criterion. From this point of view, one may envision measuring all sorts of forms of homogamy; those that are typically measured include those that are connected to the resemblances between the statuses of the future spouses or their parents (homogamy of status, even property), between professions (professional homogamy), between levels and types of education (homogamy of education), between preferences for certain activities (homogamy of cultural tastes), or even between places of residence or birth (local homogamy). The objective of this research is to try and understand the extent to which the society being studied is made up of distinct groups with more or less permeable borders⁸. In a general manner, and barring exceptions, the forms of homogamy noted by demographers correspond to "desirability of status," which includes all

⁸ Unlike their European counterparts, American studies nearly always also consider forms of homogamy linked to race and religion; that will not be taken into account here.

the individual characteristics that express a social position and therefore aim at perpetuation. What is the proportion of matrimonial choice that is not subjected to this homogamy? One can suppose that this remainder is linked, at least in part, to the other form of desirability, that which pertains only to "charm" and aims at reproduction.

If one tries to summarize the findings of demographic research, one might say that, at least where Europe is concerned, homogamy of status is stronger in the rural setting than in the urban one, and that it was stronger in the past than in the present, or more precisely, that it has changed character in the last fifty years or so. A difficulty in interpreting measurements of homogamy comes from the need to distinguish observed statistics from those that one would observe if one were in a situation of "panmixia" (random marriages): it is the difference between the two that is significant and it requires a complex calculation. Thus, the study conducted by Martine Segalen and Alain Jacquard in Vraiville, Normandy (Segalen 1970; Segalen and Jacquard 1971) was able to show that the endogamy rate varied according to time periods: it went from 55 percent during the first half of the nineteenth century to 25 percent between 1923 and 1962. Another study conducted in the canton of Chateauponsac in Limousin between 1870 and 1970 (Crognier et al. 1984) showed that the same endogamy rate varied from 44 percent in the earliest period to around 8 percent in the most recent period. In all cases, farmers were more homogamous than others, a feature that also applies to artisans in the most recent period. Nonetheless, these results should be clarified: a homogamy rate of 50 percent among farmers, for example, does not signify that farmers' children marry only farmers, but rather that half the time farmers' children marry farmers, while if the marriages occurred randomly, this probability would decrease markedly (it would fall to one in four times in the case in $point)^9$.

Studies on homogamy conducted in the modern urban setting have tended to show that homogamy has become less connected to the status transmitted by the parents, and more connected to the status achieved by the involved parties, and increasingly more connected to education level. Curiously, if one takes into account this last type of homogamy, the rate hovers around 55 percent, compared to only 30 percent for the rate related to the status of the parents (Kalmijn 1998). In France, homogamy of profession is especially strong, to the point that Michel Bozon, analyzing the 1983–1984 census, saw in it "a sharp increase in each person's social identity" (Bozon 1991). Other studies have stressed the role of equivalence of education levels between spouses, and declare an interlacing of social networks (Forsé and Chauvel 1995). Multiplying the references would lead only to confirming the features that have already been cited: a decrease in influence of social origins, but an increase in education level and type of profession in the factors leading to homogamy (Smits et al. 1999). Moreover, these regularities do not relate only to married couples, but also to cohabitating ones (Blackwell and Lichter 2000). It remains true that, in all cases, the observed homogamy is only a statistical tendency, meaning that a large fraction of the variance eludes it. For example, if one considers a study conducted in Sweden in the 1960s (Trost 1967), a period when the perception of belonging to a social class was stronger than today, homogamy of social class was at 43.8 percent, as opposed to 30.7 percent if there had been a situation of panmixia; this means that the truly relevant share of homogamy of class is 13 percent, or, in other words, that the preference for class touches a little over one in six couples. The same study shows that professional homogamy is 50.6 percent, albeit very close to the panmixia hypothesis, which is at 49.3 percent. Furthermore, the observed homogamy may simply derive from the fact that marriages are influenced by the possibilities for meeting. However,

⁹ For the period from 1803 to 1843 in Vraiville, the number of marriages noted among farmers was 28, even though there should have been only 13.6 in the case of panmixia (for a total of 114 marriages of farmers).

while these possibilities were essentially reduced to the village dance in the rural setting of the past, they are often limited in the modern world to associations due to employment.

Thus it is appropriate to note that homogamy, whatever its nature, is not the expression of a behavior that would be widespread in a given milieu and society, but a tendency that touches a fraction-sometimes substantial proportion-of this population. In other words, what has been called "desirability of status" plays a role in spouse selection; it is a role that varies in its content and intensity, a role that is significant yet partial. So what is the rest? What is this portion that is not explained by homogamy of status? Very few studies address this question. Once again, the study conducted in Sweden by Jan Trost (1967) can be cited. This study examined the convergences between attitudes before the existence of the spouses through seven traits; these traits were supposed to characterize them in a context in which the observed forms of homogamy related to age, education level, social class, political attitudes, and attitudes about relations between the sexes. The author concluded that the psychological factors at work in the choice of the spouse were perceived homogamy (that is, the manner in which each person assesses the other's position) and sexual attraction. This could not be expressed any better. Their conclusion is very similar to the proposition made here, which maintains that two forces exist: desirability of status and personal desirability. The only difficulty in the argumentation comes from the fact that although one is able to assess the former, one does not really have the means to measure the latter. This makes it difficult to determine the respective contributions of the two methods in actual choices. Nevertheless, there exists a rather clear homogamous tendency that relates to the assessment of social status, either in its property form (rural setting) or in its professional form (modern urban setting). This allows one to think that, in human societies, the desirability of status outweighs personal desirability, and leads to or strengthens social stratification. The effect of withdrawal into the—socially and culturally—similar involves a reward system that is just as social (through recognition by peers) as it is psychological (through the limitation of the unforeseen). This relative dominance of desirability of status would undoubtedly result in rigid partitioning if personal desirability did not come to distort this way of operating.

What these strategies of social withdrawal contribute to transmitting are the means to guarantee a rank in society, but these means are not infallible and they in no way guarantee that the descendants will preserve the parents' position. Furthermore, although it is clear that the abundance of available resources constitutes an advantage, this advantage is so diverse in its composition (that is, it is hardly connected to diet and health) that it does not involve any privileged relationship between reproductive ease and ability. Nonetheless, these homogamous strategies are only underlying, and one can see that a substantial share of behaviors eludes them: affairs of desire always have their chance, and it is not impossible that, from the point of view of reproduction more surely than that of perpetuation, they will ultimately have the advantage.

Sex and power are two essential elements for determining the structure of the life of relationships of animals and humans. They serve the functions of preservation and reproduction of individuals and groups. Ethologists and ethnologists have, each in their area of knowledge, analyzed, compared, and classified many social modes and individual behaviors of animals and humans. The singularities that differentiate animal species from human groups have often appeared to suffice for many authors to declare vain any attempt to compare them, and indeed, to seek similar determinisms in them. However, some authors have constructed approaches that connect ethology and ethnology, perhaps sensing that some of these differences between animals and humans might only be superficial (Lestel et al.

2006). Reproducing from the living and from the social could have as an immediate cause (proximate, the evolutionists would say) the search for satisfactions brought about by the sexual and power. The diversity and singularity of the modes of expression of these satisfactions would find their origins in the "chances and necessities" of natural or cultural evolution. Eventualities, accidents, and obligations create the framework within which reproduction and perpetuation emerge from desires and satisfactions.

Among animals and humans, reproducing from a related species is accompanied by a multiplicity of methods. Among animals, various processes make it possible to transmit life, maintain the species, and ensure a social life within groups. Among humans, mate choices make it possible not only to produce new individuals, but also to perpetuate families, cultures, and social groups thanks to the transmission of knowledge, powers, goods, and statuses. Mate choices, alliances among individuals, and parent-child relationships are means that structure and constrain social life. However, beneath this diversity observed by the naturalist and sociologist, there is an invariant principle that is at the source of reproductive and social investments, namely the search for satisfactions in order to realize desires. Animals and humans alike are beings that desire.

Bibliography

- Anderson, Malte. 1994. Sexual Selection. Princeton, NJ: Princeton University Press.
- Aragona, Brandon, Yan Liu, Thomas Curtis, Friedrich Stephan, and Zuoxin Wang. 2003. "A Critical Role for Nucleus Accumbens Dopamine in Partner Preference Formation in Male Prairie Voles." *Journal of Neuroscience* 23: 3483–90.
- Augustins, Georges. 1989. *Comment se perpétuer? Devenir des lignées, destin des patrimoines*. Paris: Société d'Ethnologie.
- Béguin, Nathalie, Gérard Leboucher, and Michel Kreutzer. 1998. "Sexual Preferences for Mate Song in Female Canaries (*Serinus canaria*)." *Behaviour* 135: 1185–96.
- Blackwell, Debra, and Daniel T. Lichter. 2000. "Mate Selection among Married and Cohabiting Couples." *Journal of Family Issues* 21: 275–301.
- Boone, James L, III. 1986. "Parental Investment and Elite Family Structure in Pre-Industrial States: A Case Study of Late Early-Medieval Modern Portuguese Society." *American Anthropologist* 88: 859–78.
- Bozon, Michel. 1991. "Mariage et mobilité sociale en France." *Revue Européenne de Démographie* 7: 171–90.
- Burley, Nancy Tyler, and Richard Symanski. 1998. "A Taste for the Beautiful: Latent Aesthetic Mate Preferences for White Crest in Two Species of Australian Grassfinches." *American Naturalist* 152: 792–802.
- Crognier, Émile, et al. 1984. *Mariage en Limousin. Évolution séculaire et identité d'une population rurale*. Paris: CNRS.
- Darwin, Charles. 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. London: John Murray.
- Darwin, Charles. 1871 [1874, 2d ed.]. *The Descent of Man and Selection in Relation to Sex*. London: John Murray.
- Draganoiu, Tudor, Laurent Nagle, and Michel Kreutzer. 2002. "Directional Female Preference for an Exaggerated Male Trait in Canary (*Serinus canaria*) Song." *Proceedings of the Royal Society Biological Sciences*, 269: 2525–31.
- Forsé Michel, and Louis Chauvel. 1995. "L'Évolution de l'homogamie en France. Une méthode pour comparer les diagonalités de plusieurs tables." *Revue Française de Sociologie* 36: 123–42.
- Hallé, Frédérique, Manfred Gahr, and Michel Kreutzer. 2003. "Effects of Unilateral Lesions of HVC on Song Patterns of Male Domesticated Canaries." *Journal of Neurobiology* 56: 303–14.
- Hara, Erina, Lubika Kubikova, Neal Hessler, and Eich Jarvis. 2007. "Role of the Midbrain Dopaminergic System in Modulation of Vocal Brain Activation by Social Context." *Journal of Neuroscience* 25: 3406–16.
- Hoquet, Thierry. 2009. Darwin contre Darwin. Paris: Le Seuil.
- Ikemoto, Satoshi, and Jaak Panksepp. 1999. "The Role of Nucleus Accumbens Dopamine in Motivated Behavior: A Unifying Interpretation with Special Reference to Reward-Seeking." *Brain Research* 31: 6–41.
- Insel, Thomas. 2003. "Is Social Attachment an Addictive Disorder?" *Physiology and Behaviour* 79: 351–57.
- Kalmijn, Matthis. 1998. "Intermarriage and Homogamy." *Annual Review of Sociology* 24: 395–421.
- Kelley, Ann, and Kent Berridge. 2002. "The Neuroscience of Natural Rewards: Relevance to Addictive Drugs." *Journal of Neuroscience* 22: 3306–11.
- Krebs, John, and Nicholas Davies. 1978. *Behavioral Ecology. An Evolutionary Approach*. Oxford: Blackwell Scientific Publications.
- Kreutzer, Michel. 2001. "Du choix esthétique chez les animaux." *Revue d'esthétique* 40: 113–16.

- Kreutzer, Michel. 2002. "Les Chants préférés des femelles oiseaux." *Pour la Science* 34: 75.
- Kutsukake, Nobuyuki. 2000. "Matrilineal Rank Inheritance Varies with Absolute Rank in Japanese Macaques." *Primates* 41: 321–35.
- Lestel, Dominique, Florence Brunois, and Florence Gaunet. 2006. "Etho-Ethnology and Ethno-Ethology." *Social Science Information* 45: 155–77.
- Lorenz, Konrad. 1958. "The Evolution of Behavior." *Scientific American* 199: 67–78.
- Marlowe, Frank, and Adam Westman. 2001. "Preferred Waist to Hip Ratio and Ecology." Personality and Individual Differences 30: 481–89.
- Marlowe, Frank, Coren Apicella, and Dorian Reed. 2005. "Men's Preferences for Women's Profile Waist-to-Hip Ratio in Two Societies." *Evolution and Human Behavior* 26: 458–68.
- Møller, Anders Pape. 1992. "Female Swallow Preference for Symmetrical Male Sexual Ornaments." *Nature* 357: 238–40.
- Parisot, Maëlle, Laurent Nagle, Éric Vallet, and Michel Kreutzer. 2004. "Dominance-Related Foraging in Female Domesticated Canaries under Laboratory Conditions." *Canadian Journal of Zoology* 82: 1246–50.
- Pereira, Michael. 1995. "Development and Social Dominance among Group-Living Primates." *American Journal of Primatology* 37: 143–75.
- Pusey, Anne, Jennifer Williams, and Jane Goodall. 1997. "The Influence of Dominance Rank on the Reproductive Success of Female Chimpanzees." *Science* 277: 828–31.
- Ryan, Michael Joseph. 1990. "Sexual Selection, Sensory System and Sensory Exploitation." Oxford Survey in Evolutionary Biology 7: 157–95.
- Segalen, Martine. 1970. *Le Choix du conjoint à Vraiville (Eure) de 1706 à 1962. Étude démographique et sociologique*. Paris: Maisonneuve et Larose.
- Segalen, Martine, and Albert Jacquard. 1971. "Choix du conjoint et homogamie." *Population* 3: 487–98.
- Slotten, Ross. 2004. *The Life of Alfred Wallace, the Heretic in Darwin's Court*. New York: Columbia University Press.
- Smits, Joroen, Wout Ultee, and Jan Lammers. 1999. "Occupational Homogamy in Eight Countries of the European Union, 1975–89." *Acta Sociologica* 42: 55–68.
- Spencer, Walter Baldwin, and Frank Gillen. 1899. *The Native Tribes of Central Australia*. London: Macmillan and Co.
- Summers, Kyle. 2005. "The Evolutionary Ecology of Despotism." *Evolution and Human Behavior* 26: 106–35.
- Suthers, Roderick, Éric Vallet, Aurélie Tanvez, and Michel Kreutzer. 2004. "Bilateral Song Production in Domestic Canaries." *Journal of Neurobiology* 60: 381–93.
- Tinbergen, Niko. 1951. *The Study of Instinct*. Oxford: Clarendon Press.
- Trost, Jan. 1967. "Some Data on Mate-Selection: Homogamy and Perceived Homogamy." Journal of Marriage and Family 29: 739–55.
- Vallet, Éric, and Michel Kreutzer. 1995. "Female Canaries are Sexually Responsive to Special Song Phrases." *Animal Behaviour* 49: 1603–10.
- Weatherhead, Patrick, and Raleigh Robertson. 1979. "Offspring Quality and the Polygyny Threshold: The Sexy Son Hypothesis." *American Naturalist* 113: 201–8.