

PERSONAL VIEW

## On sexual behavior and sex-role reversal

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### Abstract

Sex is not about reproduction; sex is about (re-)combination of DNA. Sex, not reproduction, always involves physical contact between two individuals; to achieve this, strategies of sexual behavior evolved. Sexual behavior, therefore, did not evolve as part of a reproductive strategy, but evolved to enable exchange of genetic material. In multicellular organisms the situation is more complicated than in unicellular organisms, as it is impossible for each cell within a multicellular body to have sex with another cell. Hence, evolution selected a system in which the possibility to have sex was limited to only one cell-line: the germ cells. As a result, sex adopted the character of fertilization, and sex and reproduction became inseparably linked. Still, in some species, including humans, sexual behavior still exhibits features of its evolutionary past: in humans (like in bonobo's) most sexual activity and many sexual behavioral patterns have nothing to do with reproduction (masturbation, homosexual behavior, for example); in humans, sexual behavior also became associated with other strategic objectives, such as intensifying the pair bond, expression of love or power. Different genders – male and female – evolved, and each gender evolved typical gender-related sexual and reproductive strategies as well. In most multicellular species, these strategies became inextricably mixed, and sexual behavior increasingly more – and in most species even exclusively – ‘served’ the interests of reproduction: sexual behavior became more or less synonymous with reproductive behavior. In most species, the ‘mix’ of sexual and reproductive strategies evolved into typical gender-related patterns of behavior, that is, in typical ‘sex-roles’. Often, males are bigger and more ‘beautiful’ (= more intensely ornamented) than females; males compete with each other for access to females; males court females, while females choose males (*female choice*). However, ecological circumstances may cause a reversal of sex-roles, resulting in a situation in which females are bigger and more intensely ornamented than males, females compete for access to males, females court males and only males invest in care for the young, provided they are relatively certain of their paternity. Also, as in the case of the spotted hyena, females may be highly virilized and be socially dominant. This ‘sex-role reversal’ is seen, e.g., when males are relatively rare due to high predation pressure, or when the process of reproduction is very risky for the same reason: then it is ‘better’ that males, with their plenty of sperm, are wasted, than females with their few, precious eggs. It can be argued, with women being the fair sex, exhibiting competitive behavior and with an actively displaying courtship, and with men investing heavily in their offspring, meanwhile taking all (cultural) kinds of measures to guarantee their paternity, that humans, too, exhibit some degree of sex-role reversal.

**Keywords:** *Sex-role reversal, reproductive strategy, sexual behavior, reproduction, sex*

Da werden Weiber zu Hyänen\*  
*Das Lied von der Glocke*, Schiller, 1797\*\*

### Provocation

Phainetai moi kènos isos theosin  
emmen' onèr ottis enantios toi  
isdanei kai plaison adu phonei-  
saas upakouei

kai gelaisaas imeroen to m'è maan  
kardiaan en stèthesin eptoaisèn  
oos gar es s'ido brokhe'oos phonè-  
s'ouden et'eikei

Equal to Jove that youth must be -  
Greater than Jove he seems to me -  
Who, free from Jealousy's alarms,  
Securely views thy matchless charms.  
Ah! Lesbia! Though 'tis death to me,  
I cannot choose but look on thee;  
But, at the sight, my senses fly,  
I needs must gaze, but, gazing, die;  
Whilst trembling with a thousand fears,  
Parch'd to the throat my tongue adheres,

alla kam men gloosa aege lepton  
 d'autika khrooi puur upadedromaken  
 oppatessi d'ouden orèmm' epibro-  
 meisi d'akouai

ekade m'idroos kakkheetai tromos de  
 paisan agrei khlorotera de poias  
 emmi tethnakèn d'oligo 'pideules  
 phainom' em'autai

alla paan tolmaton epei . . .

Sapho Fragment 31 (around 500 B.C.)  
 (transcribed in Roman characters)

### Sex and reproduction

When reading or listening to the poem of Sapho, the great classical Greek poetess of Lesbos, when she – jealously! – sings the praises of the girl she is in love with, one is struck by the beauty of the poetry which, as it were, reflects the beauty of the beloved girl. Clearly, female beauty may arouse strong emotions and evoke sexual feelings both in men *and* women; (sexual) susceptibility for the beauty of the female image (like that for the male image), apparently, is not limited to the 'opposite' gender.

But however lyrical the feelings female beauty may evoke, from the prosaic biological point of view, physical beauty is 'but' information, transferring a complex message to the beholder. In fact, one may ask what beauty actually *is*, as the ability to perceive beauty, after all, is a quality of the *receiver* of the message, not of the 'sender'. For if somewhere, then here holds that beauty is in the eye of the beholder, and the rational biologist realizes that because the heart of the message always boils down to the same thing, namely to the question: is the pertinent individual a suitable sexual partner?, perception of beauty is one of Nature's tricks to get things done.

Which things? Sex and reproduction. This, at least, is the situation in humans. But although already old Anaxagoras (around 500 B.C.) claimed that man is the measure of all things, biological reality is slightly different, for a sexual partner is not necessarily the same as a partner with which one reproduces, as 'sex' and 'reproduction', at least in principle, have nothing to do with each other. For sex is a cell-biological process during which two well-defined pieces of DNA (which may or may not consist of equally well-defined chromosomes, and which may or may not originate from two different individuals of (generally) the same species), fuse, whereas reproduction, at least in the end, comes down to replication of a given constellation of RNA/DNA which, in a later phase of evolution, was packed within (organelles of) cells which then replicate (divide) also.

My pulse beats quick, my breath heave short,  
 My limbs deny their slight support;  
 Cold dews pallid face o'erspread,  
 With deadly languor droops my head,  
 My ears with tingling echoes ring,  
 And life itself is on the wing,  
 My eyes refuse the cheering light,  
 Their orbs are veil'd in starless night:  
 Such pangs my nature sinks beneath,  
 And feels a temporary death

Translated by Lord Byron (c. 1820)

Only in a number of multicellular organisms, sex became linked with reproduction. Indeed, in a number of cases, e.g., in humans, the two even became inseparable. And once this was the situation, the vicissitudes of sex, including all behavioral and mental elements associated with it, mixed inextricably with those associated with the process of reproduction. This is what we see today in species such as ourselves: a very complex jumble of cell-biological and behavioral elements of different origin, yielding all kinds of selected strategies of sexual reproduction. Notably the various combinations of mental components of this mix may present surprises in humans, as every psychologist and psychiatrist knows, because like any other behavior, behavior associated with sex and reproduction too, is invariably emotionally motivated. The consequence is that sex, reproduction and emotion form an unholy trinity: the raw material of all human drama of both 'high' and 'low' culture.

Lucky the species that are not bothered by the mixing up of sex and reproduction or by the emotions associated with the existence of two different genders within one species. One such fortunate species is the unicellular, one-gender slipper animalcule, *Paramecium* sp. As discussed previously, two *Paramecium* individuals may have sex with each other, but this has nothing to do with reproduction. Simply put, *Paramecium*-sex goes as follows: two *Paramecia* nestle up against each other, and form a cellular bridge which connects their cytoplasm. The nuclei then undergo a very complex process of transformation, ultimately resulting in two haploid nuclei within each individual. Then one of the two haploid nuclei crosses the bridge to the partner, after which the haploid nuclei, now originating from each of the two partners, fuse, so that both partners become diploid again.

In a sense, this process can be compared to the fertilization process of, e.g., mammals. Here too DNA, provided by specialized germ cells, is re-combined, and here too re-combination of DNA is

not the same as reproduction; indeed, here too sex *precedes* reproduction. In *Paramecium* sex, as it were, is ‘facultative’: individuals *may* have sex before dividing, but are not ‘obliged’ to: in this species, reproduction ‘simply’ boils down to cell division, yielding two new individuals – clones, in fact. In multicellular organisms, on the other hand, reproduction comes down to a process of cell division and – differentiation of a germ cell which may or may not have been fertilized – i.e., which also may or may not have had sex – giving rise to a new individual. A striking example of a reproductive strategy involving facultative sex is provided by honey bees: female honey bees develop out fertilized oöcytes, whereas male honey bees develop out of unfertilized oöcytes, i.e., develop parthenogenetically. This however, as said, is not given to humans: in humans parthenogenesis is impossible (although various myths try to make us believe otherwise), that is, in humans: no reproduction without sex.

In fact, the mere shedding of germ cells (ovulation; spermiation) by itself can be regarded as a kind of ‘proto-reproduction’, as once the germ cells are set free, they do not belong any longer to the body of the individual that produced them, and can but die, or develop into a new individual. This, then, will yield another multicellular body consisting of two principally different compartments: germ cells and soma. This division of a multicellular body into ‘germ cells’ and ‘soma’ is the inavoidable consequence of the fact that it is simply impossible for each cell of a multicellular body such as ours to have sex with another cell; and the solution of the problem therefore, was the assignment of the noble process of sex to one cell line only – the germ cells – with the soma in the role of humble servant of (the genes within) these germ cells. Indeed, it is the soma which has the means and the strategies, necessary to enable the germ cells to have sex and form a new individual. In humans these means and strategies are very diverse, ranging from physical organs and physiological processes, to mental qualities like all kinds of cognitions, and, indeed, emotions. Endorsed with these qualities, each individual is prepared to fight its struggle for life.

### Sex roles

Because ‘sex’ evolved entirely independently of reproduction – sex, after all, concerns (re-)combination of DNA – sexual behavior, at least originally, too, had nothing to do with reproduction. Similarly, sexual behavior, at least in principle, has nothing to do with different genders either, as is demonstrated by the sexual behavior of the one-gender species, *Paramecium*. One might, therefore, even argue that the urge – known to each human being – to nestle at somebody else’s body, and to physically and emotionally unite with the other, is also not gender-related, because its evolutionary ‘ancestor’ – sex – is

older than the relatively late differentiation into two distinct genders. Still, in highly developed species like humans, differentiated into two distinct genders – male and female – and producing different germ cells – oöcytes and spermatozoa – evolution predominantly selected for heterosexual behavior, because only heterosexual behavior can lead to sex in the cell-biological sense, and hence to reproduction.

But why two different genders? Not for purposes of reproduction, but for purposes of (fusion) sex [cf. 1]. For the differentiation into two genders did not evolve as part of the process of reproduction (many species are ‘uni-sexual’): it evolved as an adaptation to some ‘nasty’ qualities of cell organelles, present in eukaryotic cells (mitochondria and, in plants, chloroplasts). For when two eukaryotic cells fuse as, e.g., the germ cells of humans do, only one of them can deliver the cell organelles, because these organelles with their prokaryotic genomes (both mitochondria and chloroplasts once were free-living bacteria; [2]) will begin a genetic conflict [3] during which they – literally! – kill each other. By definition, the organelle-delivering germ cell is the female germ cell: the oöcyte. Male germ cells do not participate in the transmission of mitochondrial DNA from one generation to the other.

The consequence of this is that we should realize that not only sex and reproduction have a different evolutionary past, but that sexual behavior and reproduction do not share a common evolutionary past, either. Consequently, one might argue that sexual behavior also – at least originally – does not ‘aim at’ reproduction. Indeed, most human beings engage in sexual behavior for reasons other than reproduction, often even taking measures *against* the possibility that they will reproduce. Moreover, human sexual behavior comprises variants which have absolutely nothing to do with reproduction: homosexual (lesbian) behavior, for example, or masturbation and the wide variety of perversities the human mind was able to invent – which is quite a lot indeed.

However, due to the evolution of multi-cellularity, ‘sex’ became increasingly more associated with reproduction (the reader should realize that next to ‘sexual reproduction’, many multi-cellular organisms are also able to reproduce a-sexually), and so became sexual behavior. Where in *Paramecium* sexual behavior still exclusively ‘served’ sex in the cell-biological sense (DNA recombination) – in organisms such as humans, that is, in organisms which obligatorily reproduce sexually, sexual behavior increasingly more came in the sphere of influence of reproduction, and reproductive strategies, selected by processes of natural and sexual selection, increasingly more ‘overtook’ the ‘motivation’ (which in most, if not all species is unconscious) to exhibit sexual behavior. Motivation, by definition, is emotional. And indeed, what we see is a co-evolution of behavioral elements ‘serving’ both sex *and* reproduc-

tion, which in humans resulted in an 'end-situation' in which sexual behavior is largely, although certainly not entirely, leavened with behavioral elements, 'serving' reproduction. A fine example of this is couples having intercourse on the doctor's advice, because they want to have a child, not because they are overwhelmed by feelings of lust.

This – rather abstract – view of the relationship between sexual behavior and reproduction may explain many phenomena considered by many as 'strange', 'abnormal' or even 'morally objectionable': phenomena like – already mentioned – masturbation, homosexual behavior etc., which, indeed, are ways of behavior in which the dissociation between sexual behavior and reproduction is plainly evident. But Nature is never impressed by the moral, philosophical or even theological considerations of us, poor mortals: Nature, like the figure of Justice, is blind and 'knows' only adaptive and mal-adaptive strategies. And what is 'strange', 'abnormal' or even 'immoral' in the eyes of those pretending to have a direct telephone line with God, may be 'normal' for all those species which happen to live under circumstances which selected quite other role patterns.

### **Courtship display: Communication and selection**

Courtship display is part of the process of mate selection and – persuasion. Persuasion? Yes, persuasion, for, as everybody knows, (potential) sexual partners do not always cherish reciprocal feelings, which may be very frustrating indeed. The principle of *female choice* adequately solves this problem – if *he* (always?) wants, and *she* chooses, *that* problem, at least, is solved – but how to make her make the right choice, that is, that she chooses *you*?

The solution of this problem demands adequate signaling. Send the right signals and her heart will melt away. And this is what courtship behavior is all about: sending the right signals. These signals, too, comprise a very complex field of information. For although humans like to believe that they select their mates because of their beauty, their wealth, their power, etc., the system in fact evolved to solve quite more important problems, i.e., the problems of gene-quality, of capability of DNA repair and of mate selection, including avoidance of inbreeding [4]. Beauty, wealth, power and the like, after all, are 'but' derivatives of 'good genes'; temporary signals, no more, for they may easily get lost.

Virtually all living organisms, from bacteria and fungi to humans, evolved communication systems capable of sending, interpreting and responding to relevant signals [4]. Chemical substances, such as yeast alpha-mating factor [5] inform the potential partner that here is an individual who is 'in the mood' for sex (interestingly, yeast alpha mating factor, a polypeptide pheromone, is chemically closely related to human gonadotropin-releasing hormone; [6]); a

similar role is played by 'pheromones' [7] or by (smelling) substances revealing the gender of another individual of the same species, as seems to be the case in ferrets [8]. Signals, however, are not only chemical by nature; they may also be acoustic (the song of birds or insects; the serenade of a latin lover), or visual (e.g., the twinkling of fireflies). These signals form part of stimulus-response systems, reflexes, which later, in so-called higher organisms like ourselves, would evolve into emotions [9], and which, both autonomously and when aroused, e.g., by the image, the smell, or just the memory of a (potential) sex partner may motivate (sexual) behavior(s).

This behavior, however, need not necessarily conform to the stereotypical ideas of those who received the Truth from Gods' own hands. For Nature – Spinoza's God – the great experimenter and adaptor, also 'invented' some quite interesting variants, sex-role reversal, for example.

### **Sex-role reversal**

#### *Anatomy and behavior*

Like any other concept, the concept 'sex-role reversion' can be broadly and narrowly interpreted, depending on the frame of reference used. If male courtship display is considered to be the rule, courtship display by females can be considered as 'sex-role reversed' behavior. If parental care by females only (as is the case in the majority of mammals) is considered to be the rule, paternal care is a kind of sex-role reversed behavior. The same holds for dominant behavior: if, in a social species, dominance by males is considered to be the rule, dominance by females is a way of sex-role reversion.

All these examples of sex-role reversion are found in Nature. The spotted hyena (*Crocuta crocuta*), for example, can be considered as a typical sex-role reversed mammal. Males and females are hard to distinguish because the genitals of the females strongly resemble those of males. Thus, female spotted hyenas, like males, have a (pseudo-) penis, derived from the clitoris which both serves as entrance to the vagina (which makes mating a kind of high-school acrobatics) and as birth canal (which makes delivery – both for the mother and the offspring – an extremely dangerous process), and a scrotum, derived from the labia majora: this all being due to high circulating levels of testosterone during pregnancy. Female spotted hyenas also have high levels of testosterone [10] and a remarkable level of aggression. Still, spotted hyenas are social animals, the leader of the group – a kind of Prime Minister – being a dominant female [11].

#### *Courtship behavior*

Sex-role reversion is also seen with respect to courting. Courting, indeed, is a very complex

behavior, 'serving' various 'goals' (once again, the reader should be reminded that Nature has no 'goals'. In fact, any courtship behavior is the result of a continuous process of natural and sexual selection, optimizing a species' fitness, that is, its reproductive success). But the main 'goal', again, is not reproduction, but sex. Courting individuals primarily 'want' sex, which, indeed, may or may not be associated with the 'wish' (or, possibly better: the (unconscious) *urge*) to generate offspring. Primarily, courtship display is communication. Hence, the question is: what is being communicated?

As we have seen: sex is about recombination of DNA. The courting individual, therefore, primarily shows that it has superior genes, that it has a superior capacity of DNA repair, and that it is able to avoid inbreeding [4]. Hence, individuals are selected for optimal transmission of information concerning these matters. Also, individuals may transfer information concerning their possible genetical 'fit' with the partner in view; in both mice and humans, the MHC system seems to play a role in this respect [12]. Individuals are also selected for their capacity to recognize these qualities. But because information concerning these qualities cannot be transferred 'directly', they have to be 'translated' into symbols that are easily to recognize. One of these symbols is 'beauty', another is symmetry (which indicates harmonious development, and hence absence of disturbing parasites and the like), and still other ones are a general appearance of health, of 'toughness' or any other talent.

Generally, but not always, males are the eager beavers. But *when* are they? For not all males seem to exhibit courting behavior directly directed to the female(s); male ungulates (deer, sheep, goat, etc.); all polygynic species, for example, prefer to compete with other males, showing that they are the best, the strongest etc. Showing to whom? Showing to the females, who 'uninterestedly' 'wait' until the winner emerges – and then mate with him. Male deer (sheep, goats, etc.), apparently, are not 'interested' in female deer; they only want to mate with them. Having done so (for a few seconds), each gender goes its way. But because it appears to work this way, male competition can be considered as a way of courtship display, because *indirectly* it aims at female attention, enabling the females to choose the winner. It is as if a golden apple inscribed 'For the Fairest' is thrown down between the males, who then, of course, begin to compete for showing *who* is the fairest. It is the principle of *female choice*, the driving force behind the process of sexual selection.

But generally, with 'courtship display' we mean male attention, directed to the female. Males draw attention with their bodily features or with their behavior, but some species (bowerbirds; *Ptilonorhynchidae*, and humans, for example), also throw artifacts (bowers with all kinds of baubles – colored

berries, for example – and jewelry, respectively) into the battle. All this means to say: 'because not only the beauty of my body and the sophistication of my behavior, but also my bower/jewels far outreaches that of my competitors, it is evident that I have the best genes, so if you are wise, you mate with me' (cf. 'my car – and not only my car! – is bigger than yours!'). To be able to display courtship in this way, male bowerbirds, like many other birds, are (at least by humans!) considered to be more beautiful than female birds, which need to be inconspicuous when they sit on the eggs. The reverse, however, i.e., females courting males, with males being the inconspicuous gender, also occurs, and is considered to present examples of 'sex-role reversal'.

Reversal of courtship behavior is not limited to birds, although birds may present the most striking examples. Typical sex-role reversed birds are the dotterel; (*Charadrius morinellus*) [13], Wilson's and the red and rednecked phalaropes (*Phalaropus tricolor*) [14], *Ph. fulicarius* [15], and *Ph. lobatus* [16], respectively), and the bronze-winged janaca (*Metopidius indicus*) [17], which all have precocial young, as well as the coucals (*Centropodidae*) which have altricial young [18]. All these species live under circumstances of extremely high predation risk such as the flat, barren tundra (dotterel, phalaropes) or certain lakes (janaca, coucals), and it is these circumstances which selected for sex-role reversal. Loss of females, after all, is always a greater disaster for reproduction than loss of males, for females produce only a few, precious eggs, while males overflow with sperm, and one male can easily fertilize several females (this is also the reason why in some countries the premium on the head of the female fox or the she-wolf was always higher than that on the head of the males). Hence, evolution selected males for taking upon them the noble, but extremely risky task of brooding and taking care of the young. And because it is in the interest of the females to 'choose' the best male (so that the chance that her precious eggs get lost is as small as possible), the females – which may be up to 50% heavier than males, and may also be more vigorous – court the males, lay their eggs, and hit the road.

Something similar is seen in pipefishes (*Syngnathidae*) [19], some species of dart-poison frogs (*Dendrobates*) [20], and even in insects like empidid dance flies (*Empidinae*) [21]. In all these cases females have more pronounced secondary sex characteristics than the males [22]; female pipefish, for example, not only are bigger than males, but also exhibit a temporary ornament which is an amplification of the normal striped pattern in these fishes. They compete with other females over males during nuptial dances, offering the males nuptial gifts [23]. This behavior (i.e., nuptial dances) is also exhibited by female dance flies, although here the situation is still 'normal' insofar as the males present nuptial gifts (midgets) to the females and not *vice*

*versa* [21]; this provides the females with the protein, necessary for egg production. As far as the offering of protein to the females is concerned, males of some species may sometimes even go to extremes, 'giving' themselves as source of food. This is what we see in the praying mantis (*Mantidae*), a 2000-species genus [24]. During mating, such males have their head bitten off by the female (a procedure which also seems to ensure effective ejaculation, albeit, fortunately, in these species only): a kind of 'Liebestod' (cf. Wagner's *Tristan und Isolde*). They may even be eaten entirely by their loving spouses in order to make sure that her protein stores are adequately supplied: a good evolutionary strategy, because once the males have done their job, i.e., have fertilized the females, they are but useless competitors for food in a world in which protein is a scarce product.

But not all sex-role reversed species became sex-role reversed due to a long process of natural and sexual selection: some are 'forced' to be so by the ultra-selfish genes of the arthropod sex-ratio distorting endoparasitic bacterium, *Wolbachia* [25] with which they are infected. This is, for example, the case in certain butterfly species, belonging to the *Acraea* family (*Acraea encedon* and *A. encedana*) [26]. Some populations of these butterflies are extremely female-biased – a result of the infection which turns males into females, like evil witches turn fair princes into toads. The infected females form lekking swarms (a 'lek' is a location where courtship behavior is displayed, and a 'lekking swarm' is a swarm of insects displaying courtship at a certain 'lek'), soliciting matings from males. Here the sex-role reversed behavior is forced upon the poor butterflies; it serves the interests of the bacterium, not of the butterflies themselves, because as an endoparasite *Wolbachia* can only pass a next generation when they are housed in a cytoplasm-containing female germ cell: male germ cells, after all, because of their lack of cytoplasm, do not present a suitable environment for them.

#### *Paternal investment*

In most species exhibiting parental investment, it is either the mother which does so (e.g., almost all mammals) or both parents (almost all birds). In some species, however, *only* the fathers exhibit parental care, e.g., some fishes (mouthbreeders) or toads, e.g., the midwife toad, *Alytes muletensis*. In this toad, both genders participate actively in courtship behavior, but the females control its course and duration, which makes this species sex-role reversed [27]. Hence, mutual participation in courtship behavior as such does not make them sex-role reversed; after all, also in other bird-species both females and males may exhibit courtship behavior (cranes, certain gulls, grebes) as well as mutual parental investment, and such species are not sex-role reversed. But if a species

exhibits *both* female courtship display *only* cq. control of mutual courtship display, *and* paternal care *only*, cq. paternal investment, e.g., defence of the nest, at the end of the breeding cycle, when costs of re-nesting (for the female) are high, as is the case, for example, in the willow tit (*Parus montanus*) [28] we may speak of sex-role reversal: paternal investment, like female courtship display, therefore, is part of "the syndrome", not its cause. The *cause* invariably lies in the circumstances under which the pertinent species have to reproduce: these circumstances select the phenotypical characteristics, among which are behavioral elements.

These characteristics may differ from species to species, probably depending on the parental investment in the offspring. First of all, as said, females try to select the best male they can get. They may, however, engage in extra-pair mating, because many sex-role reversed species are poly-androus. This selected for sperm-competition [17, 29] and, in spite of the sex-role reversal, for mate guarding, and hence for control of mating. This is the case in the spotted sandpiper, *Actitis macularia* [30; cf. 31]. But in species which are highly at risk during reproduction, and which therefore risk large investments without result, females themselves may prevent their fertilization by males of 'lower quality'. This can be seen, for example, in Wilson's phalarope [14]. The females of this female-dominated species more or less 'stalk' the male of their heart, 'jealously' guarding him similar to the way monogamic male dik-diks (*Mondoqua kirki*, a dwarf antelope) guard their partners [32], and in fact they are never fertilized by males other than their spouse, because attempts by other males are either disrupted by other, noncopulatory adults, or the females plainly reject the attempts of other males. The result is that extra-pair matings virtually never occur.

This female behavior, 'possessive' as it may seem, nevertheless is in the interest of the males, because it guarantees their paternity, always a major uncertain factor in life [cf. 33]. For only certainty of paternity warrants the enormous investments males of sex-role reversed species do; in a sense, therefore, female dominance and sex-role reversal may serve the reproductive interests of males: a truly paradoxical outcome if considered in the light of the many prejudices with which this subject is surrounded. This raises interesting questions when we look upon ourselves. If species in which the females are more beautiful than the males (beautiful in the sense of exhibiting signs or ornaments meant to select and persuade a potential (male) partner to play the game of games); in which females display courtship behavior and (try to) control it ('headaches'), and in which males heavily invest in the offspring *after* the young have been born – if, indeed, such species can be considered more or less as 'sex-role reversed', what, then, is the situation in humans?

## Humans

If considered in the light of the above, the conclusion can hardly be avoided that humans, too, exhibit some form of sex-role reversion. It is also clear that 'golden' or – even better – 'iron' rules with respect to sexual behavior do not exist: sexual behavior is, as said, a behavior in its own right, that is, a behavior which *may* be associated with reproduction, but, having a different evolutionary past, more often is not. The answer to the question why male-dominance in almost all cultures became so prominent probably is not to be found in the *sexual* strategies of humans, but in the fact that sex and reproduction became inextricably linked, so that the *reproductive* interests of men – certainty of the ever uncertain paternity [33] – began to dominate the sexual interests of women: the great tragedy of the *condition humaine*.

## Endnotes

\* Then women change into hyenas.

\*\*The Song of the Bell.

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