

## e13 Sexual selection < differential reproductive success to further the individual >

A chicken with beautiful plumage does not sit in a corner. —African proverb.<sup>2</sup>

The bulk of *Descent [of Man]*, by Darwin, 1871] deals not with human descent from apes, but with sexual selection. —Jonathan Smith.<sup>3</sup>

For Darwinians, the sine qua non of all life is procreation. What then can be said of the tail of a peacock? Artificial selection can produce features that a dispassionate appraiser would see as clearly disadvantageous to an individual's survival in the wild. Natural selection, in the best of all worlds, should refine a species.

What can be said of the tail of a peacock is that only male peacocks have them. The most successful peacock is the one that can attract the eye of the female.<sup>4</sup> The peahens are not selected for their appearance and they remain close to the average for their sex. Sexual inequality is the result. The male peacock drags around his tail.

Sexual selection<sup>5</sup> can explain sexual dimorphism.<sup>6</sup> Male elephant seals are huge (weight 1500-3700 kg) but with a billowy belly so the female (weight 350-600 kg) is not pressed to death at times of amore ashore. The biggest and most belligerent bulls are hundreds of times more successful in siring offspring because they can keep a harem of cows. The cows are the exclusive nurtures of the seal pups,<sup>7</sup> and some adopt if they lose their own.

The apparently contradictory legacy for species' fitness that differential reproductive success of the individual can bring about forced Darwin to a profound realization. This was that *evolution has to do with the success of the individual and not the species*. Should any good accrue to a species because each of its individuals seeks to leave more surviving offspring than any other then that must be entirely secondary (a point that George C. Williams hammers home in *Adaptation and Natural Selection*, 1966).<sup>8</sup> As for the unisex struggle of males for the females of their species, Darwin writes: "These struggles are generally decided by the law of battle, but in the case of birds, apparently, by the charms of their song, by their beauty or their power of courtship, as in the dancing rock-thrush of Guiana. The most vigorous and healthy males, implying perfect adaptation, must generally gain the victory in their contests. This kind of selection, however, is less rigorous than the other; it does not require the death of the less successful, but gives to them fewer descendants."

Ronald Aylmer Fisher's *runaway selection theory*, formulated in 1915, is that selection favors those males with structures (traits) that have come to attract females (see **Table e13.1**).<sup>9</sup> Though perhaps once arbitrary, the satisfied preference returns females with an evermore exaggerated preference for that structure and males with an evermore exaggeration of that structure. This evolutionary runaway process halts only when further generation to generation exaggeration of the trait threatens survival.

Gerald S. Wilkinson and Paul Reillo in 1998 have demonstrated runaway coevolution for the stalk-eyed fly (*Cyrtodiopsis dalmanni*).<sup>10</sup> In the wild, females show preference for mating with males possessing widely spaced eyes. However, this is not the inevitable tendency. Selective breeding for 13 generations evolved two lines of flies in which in one males have long eye stalks and in the other short eye stalks. Female preferences were found to coevolved with male stalk length. Females from the long-stalk line were partial to males with longer stalks, and females from the short-stalk line preferred shorter-stalked males. Apparently, female preferences are fickle and fashion driven.

Amotz and Avishag Zahavi in 1997 offered their *handicap theory* ("Only costly advertising carries its credibility on its sleeve") that structures functioning as body sexual signals are honest because they *are* a hazard to their owner.<sup>11</sup> When a gazelle sights a wolf and bounds in place high into the air with all four feet off the ground before fleeing, it is signaling that it is in tip-top condition, easily able to outrun the wolf. This stotting behavior, which tends to attract a predator's attention, is even more risky when the male carries heavy antlers. Then, as these have also cost a lot of biosynthetic energy just to grow, the male's boast is a guarantee to females. He survives *despite* such a handicap as he

has excellent other attributes. Thus the Zahavis replaces Darwin's demarkation between natural selection and sexual selection with his distinction between natural selection and signal selection.

Astrid Kodric-Brown and James H. Brown's *truth in advertising theory*, 1987, is that structures explained as a handicap by the Zahavis can sometimes double as survival tool.<sup>12</sup> When so, the costly structure is a doubly honest ad. Where found, this should be celebrated over the Darwinian model in which, what evolves to attracting the opposite sex is in itself bereft of intrinsic adaptive value.

Of extant deer (**Footnote e13.1**), moose are giants. Each year these big-nosed browsers grow antlers that can spread 2 meters.

Of extinct deer, an ice age inhabitant of Europe and Asia, *Megaloceros giganteus*, misnamed the "Irish elk" (which in Europe means "moose"), evolved males with antlers reaching 3 meters across.<sup>13</sup> The 40 kilogram weight of these according Ron A. Moen required that deposited more than 60 grams of calcium and 30 grams of phosphorus daily during their midsummer growing.<sup>14</sup> The discovery in 1819 of an almost complete skeleton (now <sup>14</sup>C dated at 9,225±95 YBP) of an adult male in marl sediments in a basin on the Ballaugh gravel fan, Isle of Man at Loughan Ruy, showed the last lived into the early Holocene. These with full-sized antlers and heads but with dwarfed bodies lived in this island refugia, isolated by rising sealevel from mainland Britain at about 10,000 YBP, where, Silvia Gonzalez speculates, mosaic vegetation could sustain small populations. Their widespread vanishing from their range across Europe to Central Asia during the Younger Dryas, has long been blamed on this 1,000-year-long cold snap in the final phase of the ice age. Then the tundra, which replaced forests, provided forage-diet with enough calcium and protein but not enough phosphorus and total calories. The balance would have been leached out of the animal's skeleton during summer and would need to be replaced later. This physiological model indicates that Irish elk with the largest racks beguiling to the females would have suffered later in the year when they could not restore their bone density or their fat reserves. Hence, big antlers are and were, even to the bitter gate of extinction, an honest ad for a well-nourished, free of parasites, mature, socially-dominant male who can also provide the female access to the best pastures and peace for them by fighting off rival males and predators (which they had done with success for 400,000 years).<sup>15</sup>

The honest advertisement rules out cheating by mimicry (otherwise common in evolution).<sup>16</sup>

In nature inequality of the sexes, should it arise, is self-reinforcing even if hidden. Male and female gametes can be indistinguishable in size and number in simple (judged to be primitive) organisms. The body plan and the formation of specific organs shared by animals as diverse as worms, insects, and mammals—including people, have their explanation in common structural genes that are ancient and cannot be shed.

Simple species, as say algae *Chlamydomonas*, have morphologically indistinguishable gametes (a condition called *isogamy* by John Merriam Kingsbury in 1964).<sup>17</sup> However, some species of genus *Chlamydomonas* have gametes of two sizes (*anisogamous*) and some produce gametes of which the egg cells are nonmotile (*oogamous*). Higher animals and plants produce morphologically distinctive male and female gametes. In sentient organisms, such as the vertebrates, the vast difference of size and number of a male's sperm to a female's egg is indicative of sexual selection.

The battle of the sexes continues after copulation, in the microscopic arena of sperm (a human male produces about 300 million per day after puberty) and eggs (a human female is with about 500 at birth and produce no more). Examples of sperm competition is in Aristotle's observation that when two cockerels of different types mated with a hen, the offspring usually resembled the male that mated second and in Charles Darwin's observation (**Footnote e13.2**) that female barnacles can shelter within their bodies as many as 14 "little husbands" each male little more than a bag of sperm. The modern study of sperm competition and sperm choice began, Tim Birkhead notes in *Promiscuity*, 2001, after Geoff Parker in 1970 enunciated the principle that if females routinely copulated with more than one male, then competition among the males would continue after copulation.<sup>18</sup>

The genes that determine male or female for these same varieties of animals are different and are opportunistic. The genetic cascade which transforms an asexual embryo into a male or female fruit fly, for example, shows no similarity to the sex-determination cascade in the worm *Caenorhabditis*

*elegans*. The advantage of sex is such that once acquired, however acquired, although it could be lost, being not a structural gene, it is conserved for a primary and a secondary reason.

In the mammalian embryo, the establishment of sexual dimorphism is under the control of both local and systemic signals. Early in fetal life, the reproductive system consists of an indifferent gonad that is indistinguishable by morphological criteria between the sexes. Adjacent to the gonads are two simple ducts: the Müllerian and the Wolffian. The development of the female requires Wnt-4, a locally acting cell-signaling molecule, which Seppo Vainio and others identified in 1999, for the development of the Müllerian duct into oviduct, uterus and upper part of the vagina.<sup>19</sup> Male gonadal differentiation is triggered by the action of Y-chromosome-encoded testis determining factor for the development of the Wolffian duct into epididymis, vas deferens and seminal vesicles.



The primary advantage of sexual reproduction, disclosed **John Maynard Smith** (1920-2004) in *The Evolution of Sex*, 1978, is that the union of two haploid (sperm and egg) cells (which is sex) even if both are partly damaged or ill mutated can result in a clean (repaired) copy of the zygote (diploid cell) of a species.<sup>20</sup> Cloning does not provide for this maintenance. The secondary advantage of sexual reproduction is that it can keep a species' diversity broad and, in what is expressed, opportunistically changeable. According to "JMS," sex in higher organisms is perpetuated, whatever its seeming cost, by the pressure that comes from sexually reproducing lowly parasites and diseases.

In rare instances, male to male accommodation can split their population into two groups—one ornamented, the other dull. This "disruptive sexual selection" is so, Erick Greene has found, for lazuli bunting (*Passerina amoena*) of North America. The yearling males of these small finches are successful in settling in territory attractive to the female with which they pair, if they are brightly plumed *and* successfully aggressive toward the brightly plumed mature male birds or dull *and* tolerant of being cuckolded by resident mature male birds.<sup>21</sup>

Human women's concealed ovulation and the limited visual similarity between offspring and father goes hand in hand evolutionarily with their polyandry in the follicular menstrual phase (when preference is for testosterone exhibiting males—square jaw, large, muscular—signaling likelihood of conception) while maintaining the advantage of ostensive monandry during the luteal phase or menses (when preference is for less male odor and more feminine faces—signaling cooperation in parental care).<sup>22</sup> Pheromone awareness in humans is via the main olfactory pathway.<sup>23</sup> (In other mammals, sniffed pheromones are additionally registered in the vomeronasal organ—two small pits or tubes behind the nostrils. During human fetal development, this organ shrinks and by birth usually contains no nerve cells.<sup>24</sup> Also, in humans the gene for the chemical mechanism of this pheromone receptor, which sends nerve signals to the brain, is mutated and nonfunctional.)<sup>25</sup>

Human defining intelligence has emerged.<sup>26</sup> Geoffrey F. Miller has postulated that this is our legacy due to the selection by females of the hunter: Hunting depends beyond mere speed, strength, and visual acuity, on a variety of cognitive skills. In observed hunter-gathering societies, skillful hunters have more offspring than the less skillful. (But beware! The presumptive in this paragraph is presumptuous of the reader missing that the inference has no hope of proof. Just so stories, though reasonable and even persuasive, are *not* science.) "Science" is a report, say, by Paul M. Thompson et al. in *Nature Neuroscience*, 2001,<sup>27</sup> that volume of brain regions containing neurons (grey-matter volume) is heritable and is strongly correlated with cognitive performance. Their study of maternal twins—who have identical genes—and fraternal twins—who share half of their genes, could differentiate between genetic and environmental factors.<sup>28</sup>

That a child has one mother is self evident but that it has one father is not. Societal mores can develop to support the one alternative wherein a child is conceived to have several biological fathers (the misconception being that a fetus keeps incorporating sperm until birth). Partible paternity is not a strange concept in 18 extant societies.<sup>29</sup> This total is from South America (for example in the Canela in Brazil, and the Curripaco and the Bari in Venezuela and Colombia), India, and New Guinea.

However, this suffices to give the lie in human evolutionary theory to stereotypes of “the coy female and the ardent male,” says Sarah Blaffer Hrdy<sup>30</sup> (refuting Darwin’s: “The female, with the rarest exceptions, is less eager than the male. ... she is coy, and may often be seen endeavouring for a long time to escape,” in *The Descent of Man, and Selection in Relation to Sex*, 1871,<sup>31</sup> and Angus John Bateman’s, 1948, principle that fruitfly promiscuity is more valuable to the reproductive success of males than to that of females and this models even humans), and to the “evolutionary bargain,” says Stephen Beckerman, in which men hunt for family food in return for guaranteed paternity.<sup>32</sup>

Confounding studies that attempt to find a genetic component for male and female behavioral differences by mapping the regions and activity of the brain is that brains are plastic, possibly throughout life. Making myth that brain cells cannot regenerate or be replaced are the findings in 1998 by Fred Gage who showed that fresh cells keep growing in the human hippocampus (learning and memory center) throughout adult life as it contains a population of neural stem cells,<sup>33</sup> and by Bradley M. Cooke, that, in mammals at least, brains change physically in response to the presence or absence of androgens (testosterone and related hormones). When adult male rats are castrated, the medial amygdala (that, because nerves from the olfactory system run into it, is believed to process odor-related cues to reproduction) is found to dramatically shrink within several weeks in volume to the size of the female rat brain *and* *visa versa* for the female given the hormones.<sup>34</sup> □

**Footnote e13.1 Cervidae (deer)** Cervids, slender legged ruminants with no front teeth (no upper incisors) are 44 species, familiar as deer, moose, elk, and caribou, and rare as *Megamuntiacus vuquangensis*, a new genus and species recently discovered in the Annamite Mountains of southeastern Asia.<sup>35</sup> Species of cervids occupy habitats, from arctic tundras to tropical forests worldwide, but are not native in Africa south of the Sahara, Australia, and Antarctica.

Antlers are bone that in spring begins to grow (covered by skin, called “velvet,” rich in blood vessels and nerves) as projections from a permanent bony base (called a *pedicel*) on the frontals. When the antlers reach full size, the velvet dies and becomes rubbed off against vegetation. In most cervids, except for the caribou, and the few species that lack antlers (but have enlarged, saber-like upper canines), only males grow antlers. Used during the fall breeding season for combat to obtain and to defend females, the antlers drop off afterwards.

**Footnote e13.2 Darwin’s barnacles** Darwin began to assemble evidence for the evolution of species in 1837 but became concerned that his ideas would not be taken seriously unless he was already a respected scientist. He had been inspired to zoological discovery while 16 years of age at Edinburgh University by **Robert Grant** who had taken him on a seacoast collecting expedition. Later, his first recognition as a naturalist was an acknowledgment in James Francis Stephens (1792-1853) *Illustrations of British entomology*, 1829,<sup>36</sup> of his helping, while at Cambridge University, Henslow in tracking down insect species. So for the years 1846-54, upon the sage suggestion of his confidant J. D. Hooker, he devoted himself to the study of barnacles (Cirripedia). Some he had collected during his voyage on the *Beagle*. Others, living and fossil, he borrowed from the British Museum zoological collections and received from compliant correspondents around the world. His absorbed eight-year study of this small marine creature that attaches itself to the hull of boats and other substrates, produced surprises—especially with regard to the bizarre sexualities of the species—that filled a well received (and correctly mostly dull) four-volume tome published 1851-54.<sup>37</sup>



**Robert Edmond Grant (1793-1874)** in 1828 became the first professor of comparative anatomy and zoology at University of London, the world’s first secular university, founded in 1826. He received international acclaim for work on sponges, sea pens and mollusks. Darwin in his “Historical Sketch” in the third edition of *Origin* paid tribute to Grant’s Lamarckian ideas on the origin of species, such as that higher life descended from sponges (false).