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Sexual Selection and the Origins of Human Mating Systems

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In 2009, biologists celebrated a double anniversary for Charles Darwin – two centuries after his birth and 150 years along from publication of *On the Origin of Species by Means of Natural Selection in the Struggle for Life*. That title specifically emphasized the fundamental process of natural selection, a concept that changed biology forever. Natural selection essentially boils down to differential reproductive success. So it is odd that scientific treatments of human evolution often give scant attention to reproductive biology. This is no doubt partly due to the fact that the fossil record has little to tell us about the evolution of human reproduction. Nevertheless, reproduction is a key topic that deserves serious academic treatment. So Alan Dixson's new book *Sexual Selection and the Origins of Human Mating Systems*, written as an explicit accompaniment to the Darwin celebration, is most welcome.

Dixson's background is ideally suited to the task of reviewing the evolution of human mating systems. He has directly studied an impressive spectrum of primates, ranging from bushbabies to gorillas, and has worked in the field as well as in the laboratory. Originally trained in zoology, Dixson investigated reproductive biology of primates for his PhD research at the University of Birmingham. Subsequently, he steadily established himself as a leader in comparative studies of reproductive biology and the evolution of sexuality in primates and other mammals. During his career, he has held research appointments at the Zoological Society of London, the Medical Research Council in Edinburgh, the International Medical Research Centre in Gabon, the Sub-Department of Animal Behaviour at the University of Cambridge and the Center for Research on Endangered Species at the Zoological Society of San Diego. He currently holds a professorship in the School of Biological Sciences at Victoria University in Wellington, New Zealand. Drawing on a substantial body of original scientific papers, in 1998 Dixson published an influential textbook entitled *Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes and Human Beings* (Oxford, Oxford University Press). That book (a revised edition of which is reportedly in the pipeline) assembled the sturdy comparative framework required for the more specific focus in *Sexual Selection and the Origins of Human Mating Systems*.

It has to be said that there is a thriving literature that addresses various aspects of the evolution of human reproduction, but it is largely designed for a popular audi-

ence. This is all well and good, but it is a golden rule that popular presentations should follow in the wake of serious scientific studies. And therein lies the rub. As already noted, serious scientific studies of the evolution of human reproductive biology are few and far between. So it is perhaps hardly surprising that a self-reinforcing popular mythology has grown up. Various notions that have no firm scientific support, and indeed often directly conflict with available evidence, have become common currency. A frequent approach is to take a few purportedly unique features of human reproduction – absence of oestrus, concealed ovulation, female orgasm and the like – and to concoct an appealing scenario to ‘explain’ their evolution and particular significance. How I have longed for a serious review of the large body of comparative evidence that has accumulated over the years! And this is precisely what Dixson’s new book provides, with the added bonus that he himself has made major contributions to the wealth of comparative data that is now available.

In a relatively brief text of less than 200 pages, backed up with a comprehensive bibliography listing some 700 references, Dixson succinctly distills comparative evidence from anatomy, reproductive physiology and behaviour relating to human reproduction. His initial chapter (‘A glance at the terrain’) provides an outline review of the fossil evidence for human evolution as a backdrop for subsequent chapters dealing explicitly with reproductive biology. Chapter 2 (‘Making holes in the dark’) focuses on relative size of the testes and the associated notion of sperm competition as key indicators of mating arrangements. Interesting information on paternity, including human data, is also provided. Contrary to popular mythology – often invoking ‘unpublishable’ incidental genetic findings from dissolute housing estates – human extra-pair paternity is actually quite limited, at least in the USA and Europe. The theme of sperm competition is continued in chapter 3 (‘Masculine dimensions’), which examines the structure of spermatozoa and various dimensions of the male reproductive tract, including penis size. One problem with arguments based on testis size is that the direction of the causal relationship is uncertain. A male’s mating activities might influence the size of his testes. (This could account for the reported variation between human populations, a point that Dixson fails to make.) It was therefore quite a breakthrough when Dixson, together with colleague Matt Anderson, reported in *Nature* in 2002 that the size of the sperm midpiece containing the mitochondrial ‘fuel tank’ is clearly linked to the level of sperm competition. (I am prepared to bet that the size of the sperm midpiece does not vary significantly between human populations.) Additional information from other features of the male reproductive tract, such as dimensions of the vas deferens and development of accessory glands, rounds off a very convincing interpretation of mating arrangements in primates. From this, it is quite clear that – contrasting with our closest relatives the chimpanzees (and with various published fantasies) – we humans are not adapted for a mating system in which sperm competition is prevalent. It is abundantly clear that humans are not biologically equipped for a multi-male mating system. However, it is not easy to choose between the two alternatives for single-male mating: monogamy or polygyny.

Chapter 4 (‘Cryptic female choices’) turns to dimensions of the female reproductive tract, such as the length of the vagina and of the oviduct. These female dimensions yield complementary indications of adaptation for mating arrangements and broadly confirm conclusions drawn from dimensions of the male reproductive system. The process of sperm migration from the vagina to the site of fertilization is

reviewed as well. This chapter also discusses the female orgasm and firmly dispels the myth that it is unique to humans. Numerous studies have shown that female orgasms occur in various monkeys and apes. This is a classic instance where abundant speculation has been based on an erroneous attribution of uniqueness to the human female. Chapter 5 ('Copulatory patterns') provides a survey of copulatory postures, frequencies and durations from a broad primate perspective. Dixson infers a copulatory pattern for ancestral hominoids that involved a single brief intromission and pelvic thrusts and no genital lock. Once again at odds with popular mythology, available data indicate that copulation in humans typically lasts only a couple of minutes. Chapter 6 ('The oestrus that never was') demolishes two more popular myths. It is convincingly demonstrated, with numerous examples from ovarian cycles and mating behaviour of non-human primates, that neither the absence of oestrus nor concealed ovulation is unique to the human species. Classical mammalian oestrus was probably lost in the common ancestor of monkeys and apes. Previous scientific publications have repeatedly noted this, but the myths live on. Chapter 7 considers the special topic of sexual dimorphism, which provides an additional source of information regarding mating systems. Dimorphism is essentially absent from pair-living primates with monogamous mating. Here is one of the rare cases in which fossil evidence can provide relevant information. This wide-ranging chapter also provides an effective review of findings concerning mate attractiveness in humans, covering such aspects as the waist:hip ratio in women and facial features (including male beards). In a similar vein, chapter 8 ('Adam's apple') goes on to consider sexual differences in vocal adaptations in a comparative context. Interestingly, evidence from mild sexual dimorphism in body size and differences in muscularity, body hair, facial appearance (with beard growth and pattern baldness in men) and vocal features between men and women all indicate mild polygyny, rather than monogamy, as the basic biological adaptation for human mating. In his closing chapter 9 ('The road to truth'), Dixson pulls together the various threads from previous chapters to weave a convincing set of conclusions.

One of the advantages of effective reviews is that they highlight points that were not previously evident. Dixson's careful compilation of evidence relating to sexual dimorphism provides one good example. His figure 7.3, a plot of body size dimorphism against socioeconomic sex ratio, is based on a recent comprehensive data set. Yet a few pages previously, figure 7.1 shows an oft-repeated diagram (attributed to Clutton-Brock, 1991) comparing degrees of dimorphism in body size and canine size in primates according to mating system. Figure 7.1 indicates that body size dimorphism is more pronounced in polygynous primates than in those living in multi-male groups. Yet figure 7.3 reveals that this difference disappears when a more comprehensive data set is examined. So the Clutton-Brock diagram clearly requires updating.

All in all, *Sexual Selection and the Origins of Human Mating Systems* is an engaging and informative compendium. I strongly recommend it to all those who prefer scientific fact to popular mythology.

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