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Animal homosexuality in evolutionary perspective

More often than not, great scientific journeys start with a paradox. For instance, Charles Darwin was intrigued by the non-reproductive castes of some insect species, to the extent of considering them a major obstacle to his theory of evolution by natural selection. In the sixth edition of *The Origin of Species* he wrote:

> I will not enter on these several cases, but will confine myself to one special difficulty, which at first appeared to me insuperable, and actually fatal to the whole theory. I allude to the neuters or sterile females in insect communities: for these neuters often differ widely in instinct and in structure from both the males and fertile females, and yet, from being sterile, they cannot propagate their kind
>
> (Darwin 1872a).

The search for a resolution to Darwin's sterile castes paradox produced a wealth of research that mainly took off in the 1960s and 1970s and that from the elegant William D. Hamilton's formula (also known as *Hamilton's Rule*) and John Maynard Smith's concept of kin selection, through Edward O. Wilson's impressive *Sociobiology: The New Synthesis*, has led us nowadays to *Reproductive Skew Theory*.

More than 80 years after Darwin's formulation of his non-reproductive castes paradox, the ecologist George Evelyn Hutchinson (1959) was able to turn the apparently most trivial of questions: 'Why are there so many kinds of animals?' into a major evolutionary ecological paradox leading to the study and better understanding of the ecological processes, such as interspecific competition, that determine the structure and dynamics of natural communities. Over evolutionary time, such ecological processes can eventually produce character displacement and, ultimately, speciation.

In the early 1970s it was the turn of sex to become paradoxical. When John Maynard Smith (1971) enquired about the origin of sex in his *The Origin and Maintenance of Sex*, what he meant was the origin of sexual reproduction: Why should some species reproduce sexually, a process that implies a 'waste' in reproductive capacity in the form of males, rather than asexually as parthenogenetic species do? In other words, Maynard Smith was able to transform heterosexual sex, and here I want to stress the word *heterosexual*, into an evolutionarily paradoxical phenomenon. In the same way as even heterosexual sex, i.e. the *prima facie* most unparadoxical of biological phenomena because it can lead to reproduction, can be seen as a paradox, homosexual sex has also gained in recent times the status of evolutionary paradox.

Homosexual behaviour can be defined as an interaction that is ***sexual or of sexual origin*** and that is performed between two or more individuals of the same sex. Homosexuality, in turn, is a sexual orientation that is characterised by sexual attraction to individuals of the same sex. Leaving internal mental states aside for a moment, from the perspective of manifest behaviour, the *attraction* involved in the definition of homosexuality may imply exclusive, sometimes life-long, preference for engaging oneself in sexual behaviours with members of the same sex, or shorter-term experiences. In other words, an individual who usually mates heterosexually but who does mate homosexually if, for instance, only individuals of the same sex are available is behaving in a homosexual fashion in the latter circumstance. If the behaviour is freely expressed, then some degree of attraction may also be involved. Whether it is exclusive or occasional, in all those cases individuals are described as behaving homosexually, but the differences between one and the other should obviously be acknowledged and studied.

In studies of homosexuality, *sexual attraction* and *sexual behaviour* are two distinct phenomena that should be the target of specific empirical research. For instance, in humans consensual occasional homosexual behaviour may also involve temporary same-sex sexual attraction, but if the occasional homosexual behaviour is performed under coercion (e.g. in a prison), it may not involve sexual attraction by one of the two partners; on the other hand, individuals exclusively attracted to members of the same sex may engage in sexual behaviour with members of the other sex under specific circumstances (e.g. social pressure to marry, but also desire to have a child). Whereas homosexual behaviour is a major focus of this book, sexual attraction aspects of homosexuality are explicitly identified here in the context of empirical studies carried out across various species, including humans, that involve the opportunity to choose at the same time between male and female sexual partners. All of these complexities are encapsulated in the definition of homosexuality. An interesting historical study of the definition of homosexuality can be found in Sell (1997).

At this point I also have to mention the concepts of bisexuality and bisexual behaviour. Bisexuality involves sexual attraction towards members of both sexes, attraction that will be expressed in sexual behaviour performed with members of both the same and the other sex. Such sexual attraction for and sexual behaviour performed with members of both sexes may be concurrent (*simultaneous bisexuality*; Weinberg *et al.* 1994), i.e. the individual may engage in sexual activities with either males or females, or homosexuality and heterosexuality may represent non-overlapping phases in the individual's lifespan (*sequential bisexuality*; Weinberg *et al.* 1994). In the latter case we have a situation where an individual is either homosexual or heterosexual during specific periods of his/her life, but bisexual over the lifetime. The example of the 'occasional homosexual' that I mentioned above should be more appropriately described as a case of sequential bisexuality.

Manifest behaviours are also associated with mental states that are more accessible in some species (e.g. in humans through language) than others, with gender identity, or self-definition of own gender, being especially dependent on language in humans. In this book the focus will be on manifest behaviours and on mechanisms that can cause, proximately and ultimately, the maintenance of, but also changes in, those behaviours. Whether similarities in behaviours across species are associated with similarities in internal mental states such as gender identity or not is an issue of no easy resolution. Given the current difficulties of studying sexual identity in a cross-species comparative perspective, the emphasis in the various chapters will be more on sexual behaviour, sexual orientation (homosexuality, heterosexuality, bisexuality) and gender role (masculinity, femininity, androgyny) than on identity.

The **evolutionary paradox** of homosexuality can then be formulated in this manner: *If sexual behaviours such as mounting or genito-genital contact have originally evolved in the context of reproduction, why is it that they occur between members of the same sex where those behaviours cannot obviously lead to immediate fertilisation?*

The aim in this book is to try to resolve the evolutionary paradox of homosexuality. As suggested by Richard Dawkins (1982) the paradox is especially intriguing whenever homosexual behaviour is found to be heritable. The behaviour is also especially intriguing from an evolutionary perspective when the individual is an exclusive homosexual and actively prefers to engage sexually with conspecifics of the same sex given a choice of sexual partners. The assumption, implicit in the definition of the evolutionary paradox of homosexuality, that *mounting or genito-genital contact have originally evolved in the context of reproduction* is amply supported by the widespread direct association of mounting behaviour with fertilisation, whereas mounting performed in social interactions not associated or only indirectly associated with the act of fertilisation, although not uncommon, is nevertheless relatively less widespread in animals.

Throughout this book homosexual behaviour, same-sex sexual behaviour, and isosexual behaviour will be regarded as synonyms. Alternative terms to *homosexuality*, such as androphilia and gynephilia or gynecophilia (see, for example, Vasey *et al.* 2007; Diamond 2009), that refer to the orientation of individuals who are sexually attracted to males or females respectively independent of their own sex, and alternative terms to *homosexual* such as 'women who have sex with women' and 'men who have sex with men' that are increasingly common in the medical and psychological literature to emphasise the behaviour more than the gender identity, are also acknowledged and sometimes used in this book. Some of the authors that are quoted have also used the terms 'gay man' and/or 'lesbian' in their works and their choice of lexicon has been maintained in the text; however, in all cases the terms are used in this book simply to mean male and female homosexual, independently of any additional cultural, political or philosophical meaning that the terms may have. Interestingly, the term *queer* (see, for example, Jagose 1996), which took on a connotation of 'homosexual' in the late nineteenth century, although it has been more or less consistently in use since the 1990s (Sell 1997), nevertheless appears infrequently in the current scientific literature on homosexuality. Finally, I decided to spare the reader any lengthy discussion of the pros and cons of the use of one or the other term; they all have some positive and some negative aspects with regard to their usefulness in the study of homosexuality. The terms used in this book are defined in the text and in the Glossary (see Appendix 1) and the usage strictly adheres to such definition.

Although homosexual behaviour in our own species will obviously feature prominently in this book, it is our intention to approach the study of human homosexuality in a comparative manner. The particular focus is on mammals and birds, the two behaviourally most complex classes of vertebrates, which, however, are separated by a period of about 250 million years of independent evolution. What will be shown in this book is that same-sex sexual behaviour is more common among mammals than among birds and that although those two taxa display some similarities in the modalities of same-sex sexual behaviour, they also show many differences.

In the following sections I provide a historical overview of the study of homosexual behaviour, then list the major hypotheses that have been proposed to explain homosexual behaviour at different levels of analysis and causation. Finally, I briefly describe the plan of the book and the contents of the remaining chapters.

Historical overview of studies on homosexual behaviour

The scientific study of homosexual behaviour and orientation has come a long way since its initial steps in the nineteenth century. Today regular scientific meetings are organised and journals are published that report and discuss the findings of state-of-the-art research (see, for example, Zucker 2008a; Patterson 2008). At the broader community level, scientific initiatives such as the exposition about homosexual behaviour in animals organised by the Oslo Natural History Museum in 2006 (British Broadcasting Corporation 2006) and press releases regarding specific cases of same-sex sexual behaviour in animals (e.g. Smith 2004), in spite of their shortcomings, do help in closing the gap between scholarly research on sexual behaviour and orientation across the animal kingdom and the broader community. Undoubtedly, such initiatives help to dissipate the mist of taboo that still engulfs sections of our society, including sections of the professional scientific community, regarding evolutionary research on homosexuality.

The term *homosexuality* was coined by Karl-Maria Benkert, an activist for the cause of the civil rights of homosexuals, in 1869. Benkert wrote under the pseudonym, later to become his legal surname, of Karl-Maria Kertbény (Herzer 1985; Byne & Parsons 1993), a choice that is usually interpreted as an attempt by Benkert to make his surname sound more Hungarian, although it is an interesting coincidence that he chose such a surname at a time when homosexuals were referred to as 'inverts', a concept first introduced in sex research by Carl Westphal (1869). Other terms that were in common use in the nineteenth century and that referred to same-sex sexual behaviour included: Casper's *paederasty*, Ulrichs' *uranianism* (Ulrich referred to homosexuals as 'urnings'), Westphal's *contrary sexual feeling*, Hössli's *man-love*, Heismoth's *homophily* and Römer's *homoiophily* (Herzer 1985). Vern L. Bullough (2004), in his biographical article on Alfred Kinsey published in the *Archives of Sexual Behaviour*, made the interesting point that many of the sex researchers who were more or less Benkert's contemporaries in the period between the end of the nineteenth and beginning of the twentieth centuries were German-speaking Jewish physicians. His explanation for this is worth a full quote and it should be a matter for some meditation:

> One reason for this Jewish predominance was not so much their more positive attitudes about sexuality than the Christians of their time, but the fact that in Germany Jewish physicians were discriminated against in many of the developing specialities and denied university appointments although they could attend university. Investigation into sexuality gave them an opportunity to explore new fields and to gain new insights into patient well-being, independent of the university
> (Bullough 2004: 278).

What I want to highlight with this quote is that a novel, controversial, and yet socially important field of inquiry was, at least in part, relegated to somehow marginalised communities of researchers, according to Bullough, perhaps because most of the academic establishment was too afraid to take risks? One is only left to wonder how much things have really changed since then in universities around the world (see Kempner 2008).

According to Hubert Kennedy (1997) it was Karl Heinrich Ulrichs who first proposed a scientific theory of human homosexuality between 1864 and 1865. Ulrichs viewed homosexuality not as a pathological condition, but as a 'riddle of nature' (Herzer 1985). Ulrichs' theory emphasised other-sex sex role and other-sex sexual identity aspects of homosexuality: *anima muliebris virili corpore inclusa*, 'a woman's soul trapped in a man's body' in the case of males and, for females, *anima virilis muliebri corpore inclusa*, 'a man's soul trapped in a woman's body', an unfortunate bias that still permeates many of the current studies of homosexual behaviour in humans and other animals. Although Ulrichs ultimately preferred to see homosexuals as a 'third sex', a view shared with Magnus Hirschfeld (1914; see also Crozier 2000), later in life he also recognised the occurrence of both masculine and feminine male homosexuals (Kennedy 1980/81).

The inversion model of homosexuality was also supported by other early students of sexual orientation such as Sigmund Freud (1905), Richard von Krafft-Ebing (1886) and Henry Havelock Ellis (1928, see also Crozier 2000, 2008). Masculine and feminine gender roles vary, however, and they may be affected by interactions with the external social milieu and other environmental components during development. They can also vary more or less independently of sex and sexual orientation. Masculinisation and de-feminisation, feminisation and de-masculinisation are distinct processes of development (Money 1987). The gender role inversion view of homosexuality has been rejected by various authors (e.g. Kinsey *et al.* 1948; Veniegas & Conley 2000; Peplau 2001), as the combinatorial capacity of gender roles can explain an almost continuous gradation of masculine, feminine and androgynous characteristics among homosexuals, heterosexuals and bisexuals within and across cultures (Kinsey *et al.* 1948; Bem 1974; Shively & De Cecco 1977; Ross 1981; Storms 1981; Whitam 1983; Klein *et al.* 1985; Bem 1987; Deaux 1987; Maccoby 1987; Weinrich 1987; McCabe 1989; Cramer *et al.* 1993; Peters &

Cantrell 1993; Stein 1999; Kauth 2000; Lippa & Tan 2001; Kauth 2002; Dewar 2003; Roughgarden 2004).

Another recurrent idea that is still entertained by some even today is that the development of a homosexual sexual orientation is favoured by masturbation at early ages (see Martin 1993 for a review), an alleged causal link that took hold only at the beginning of the twentieth century with the rise of psychoanalysis (Martin 1993). We will see in this book that there is no comparative evidence for a direct causal link.

The distribution of sexual orientations within the human population has also been the battleground of significant intellectual clashes that drag on even today (Crozier 2000). Krafft-Ebing (1886) favoured a bimodal distribution with peaks formed by homosexuals at one end and heterosexuals at the other, a view subsequently also supported by Rado (1940). More recently, a bimodal view has been embraced by LeVay (1996), Pillard & Bailey (1998), Rahman & Wilson (2003a) and Rahman (2005a). Other authors see the distribution of sexual orientations as continuous and multimodal, with bisexuality being a proper sexual orientation that can be significantly represented in the adult population, rather than an unstable transient state in the progression from heterosexuality to homosexuality (Fliess 1897 (cited in Sulloway 1979); Moll 1897; Freud 1905, 1931; Hirschfeld 1914; Kinsey 1941; Bell & Weinberg 1978; Wilson 1978; McConaghy 1987; Ruse 1988; Money 1990; Gorman 1994; Van Wyk & Geist 1995; Kirk *et al.* 2000; Kirkpatrick 2000; Peplau & Garnets 2000; Peplau 2001; Dewar 2003; Kangasvuo 2003; Adriaens and DeBlock 2006; Diamond 2008b; Worthington & Reynolds 2009). The multimodal distribution of sexual orientations among humans has been especially highlighted by the recent empirical works of Weinrich & Klein (2003) and Worthington & Reynolds (2009), whereas Stokes *et al.* (1997) provided empirical evidence that the majority of male bisexuals in their sample remained bisexuals (49%), whereas only some of those bisexuals made the transition to full homosexuality (34%) and an even smaller proportion (17%) made the transition to full heterosexuality.

One of the major criticisms of human sexuality studies carried out in the late nineteenth and the early twentieth centuries is that they were based, with only a handful of exceptions (Gathorne-Hardy 1998: 152), on the in-depth analysis of a small number of case studies, and from those limited cases psychologists derived some very impressive theoretical constructs. In principle, there is nothing wrong with considering single-case studies, as they may be seen as the ‘first line of evidence’ (Levin 2007) in the testing of a theory. However, the theory that was inspired by the limited sample of cases subsequently needs to be subject to stringent empirical tests that usually require larger sample sizes. It was not until the middle of the twentieth century that such a necessary step in the testing of theories of human sexuality was taken at a scale that allowed proper statistical analyses to be carried out. It is generally acknowledged that the *Kinsey Reports* (Kinsey *et al.* 1948, 1953) are a real turning point in the study of homosexuality (Bullough 2004). Interestingly, Alfred Charles Kinsey was a graduate in both biology and psychology who, after starting his scientific career as a zoologist, finally ended up heading the most ambitious study of the various aspects of human sexuality undertaken until then. This was based upon the collection of face-to-face, in-depth interview data (Gathorne-Hardy 1998; Bullough 2004). His dataset included more than 18 000 case studies collected in the USA, a very impressive number by anyone’s standards. Kinsey’s works, including the *Kinsey Scale,* will be mentioned in various chapters of this book. Incidentally, I should point out that a conceptualisation of sexual orientation as a continuum of states had also been expressed in a scale fashion by Magnus Hirschfeld 40 years before Kinsey did the same (Brennan & Hegarty 2007).

Kinsey founded what is now known as the Kinsey Institute for Research in Sex, Gender, and Reproduction in 1947 at Indiana University (USA); extremely valuable summary statistics on various aspects of human sexuality collected from diverse sources can be freely accessed from the Institute at www.kinseyinstitute.org/resources/FAQ.html. Among many other contributions, Kinsey identified and quantified a variegated distribution of sexual orientations ranging from strict heterosexuality to various degrees of bisexuality to strict homosexuality. The importance of Kinsey's work in highlighting the relevance of human bisexuality – it is possible that he might have been bisexual himself (Gathorne-Hardy 1998) – has recently been acknowledged by the *Journal of Bisexuality,* which in 2008 devoted an issue to the commemoration of the sixtieth anniversary of the publication in 1948 of Kinsey, Pomeroy and Martin's *Sexual Behavior in the Human Male* (Suresha 2008).

Bisexual sexual behaviour is far from uncommon in human populations, with estimates ranging from 1.8%–33% in men and 2.8%–65.4% in women (Kinsey *et al.* 1948, 1953; Hunt 1974; Janus & Janus 1993; Mosher *et al.* 2005; Francis 2008; Santtila *et al.* 2008; see Blumstein & Schwartz 1977; Morrow 1989; Pryor *et al.* 1995 for reviews). This suggests that the distribution of sexual orientations in most human populations is not bimodal (see also Weinberg *et al.* 1994). A bimodal distribution may be trivially obtained through straightforward sampling biases, for instance, if one is looking for exclusive gay/lesbians and exclusive heterosexuals for strict methodological purposes associated with the aims of the study (see, for example, Hamer & Copeland 1994) or if participants in the study are recruited from specific sources where bisexuals are hard to find. More importantly, a bimodal distribution of sexual orientations, when it occurs, may be a potential result of social factors such as the political polarisation of heterosexuals and homosexuals (Weeks 1985; Jagose 1996) that may squeeze bisexuals out of the public arena (see, for example, Balsam & Mohr 2007; Diamond 2008b). In fact, Shively and De Cecco (1977, cited in Feldman 1984) noted a decrease in the reported frequency of bisexuals between the early (1940s–1950s) Kinsey reports and the later report of 1978 (Bell & Weinberg 1978). Although this shift could be interpreted as a greater tendency for homosexuals to 'come out' during the 1970s, the alternative that the admission by an individual of being bisexually oriented might have been affected (e.g. suppressed) in the 1970s by political polarisation should also be explored (Weinberg *et al.* 1994 make a similar point in a study that analysed data collected in the 1980s).

More recently, Balsam & Mohr (2007) have suggested that, although bisexuality can be a stable sexual orientation, its stability may be jeopardised by the level of prejudice and stigma against bisexuals coming from both heterosexuals and homosexuals in the community. In the case of women, Lisa Diamond (2008a) has recently reported a trend for an increased level of heterosexual–homosexual bimodalism in the distribution of sexual behaviour over time (i.e. as the respondents aged) in a group of women interviewed regularly between 1995 and 2005. She interprets such a trend as a result of the subjects increasing the level of stable, long-term partnerships with age. The distributions of sexual attraction, rather than sexual behaviour, however, were more even (i.e. less bimodal) and did not change dramatically during the 10-year period of the study. As suggested above, this discrepancy between actual behaviour (bimodal) and attraction (more evenly distributed) may well be a result of increased political definition in the public sphere as women mature. However, Diamond's (2008a) alternative explanation, that behavioural bimodality is a necessary outcome of increased long-term monogamous partnerships across sexual orientations as individuals age, is also plausible (see also Weinberg *et al.* 1994b). Overall, Diamond too supports a variegated distribution of sexual orientations among women, with bisexuality being a proper sexual orientation rather than a transient state (see also Sanders *et al.* 2008).

Among men, a shift against an otherwise desired state of bisexuality has also been explained by respondents as a strategic decision motivated by various factors, including lack of social support – from family, gay groups, heterosexual members of society at large – for a bisexually oriented person, and the need to establish a monogamous relationship (Weinberg *et al.* 1994b; Matteson 1997 make similar points). In an excellent recent work authored by Eric Anderson (2008) some respondents engaged in rather interesting semantic juggling in order to reconcile heterosexuality and same-sex sexual behaviour without mentioning the word 'bisexual':

> 'And when I asked if he thought men who have sex with men are gay he said, 'Not really, no. They can be, but don't have to be. *And gay men can have sex with women too*. It doesn't mean they are straight'
>
> (Anderson 2008: 111, italics mine).

Anderson obviously does realise that there is an issue here:

> 'Interestingly, none of the men in either group used the label of bisexuality to describe their sexual identities either. I suggest this reflects either a defensive maneuver to protect themselves from higher rates of bi/homophobia outside of cheerleading culture or a growing polarization of sexual categorization among men in this age cohort more broadly'
>
> (Anderson 2008: 112).

In this context, it is also worth mentioning the work of Carrier (1985) on Mexican male bisexuality. Although in Mexico masculine and feminine gender roles are quite well defined, when it comes to sexual intercourse, same-sex sexuality is well accepted and widespread among men, with the inserter individual retaining his full masculinity in the prevailing cultural stereotype. Most men who have sex with other men do also have sex with women, a pattern that defines them as bisexuals. According to Carrier (1985) such activities are, at least in part, a result of the cultural practice of female chastity before marriage, and their social acceptance, at least in the case of the inserter individual, removes an important barrier to their widespread occurrence. An equivalent system is found in the Brazilian state of Santa Catarina, where feminised male homosexuals known as *paneleiros* engage in sexual intercourse with masculinised *paneleiros lovers*, who are functionally bisexual men (Cardoso 2005), and also in Independent Samoa where mostly feminised males known as *fa'afafine* have sex with masculinised men especially when women are not easily available (Vasey *et al.* 2007).

Although Cardoso (2009) suggests that masculinised men participating in sexual intercourse in an 'active' (mounter) role with feminised men – who assume a more 'passive' (mountee) role – do not self-identify as homosexuals across many cultures, in my opinion they none the less do qualify as bisexuals. Moreover, it still remains uncertain whether they would change their opinion about their own sexual orientation and identity were social pressures and prejudice against homosexuals and bisexuals eliminated. We will see in Chapter 8, however, that a heterosexual self-identification of males adopting a mounter role in occasional homosexual sexual encounters is also consistent with an ancient socio-sexual role of same-sex sexual behaviour, a role that may be adaptive in the context of dominance and/or cooperation across many taxa, including many primates. Purely hedonistic aspects of the sexual act may also play a role, of course. Such an evolutionary scenario, however, is also fully consistent with a bisexual self-identification. For instance, the practices of ritualised homosexuality that will be mentioned below (Herdt 1984a) would not be possible unless human sexual orientation included an important component of bisexuality.

Rieger *et al.* (2005), in a recent work, also accept the occurrence of male bisexuality in terms of behaviour and identitity, but question its reality in terms of sexual attraction and arousal towards both males and females. They carried out an empirical study in the USA where 30 heterosexual, 33 bisexual and 38 homosexual men viewed a neutral film (e.g. a landscape) for 11 minutes, then the participants were exposed to various sexual films for two minutes, followed by a neutral film again. The sexual films showed either two males or two females engaged in sexual intercourse. The authors measured sexual arousal through both the degree of penile erection recorded during the screening of the various films and also the level of subjective sexual arousal expressed by the participants. Subjective arousal did show an increase for the least preferred sex in participants falling into the bisexual sexual orientation region, as measured by the *Kinsey Scale*. Heterosexuals and homosexuals showed low subjective sexual arousal when shown films involving the least preferred sex (i.e. males for heterosexuals and females for homosexuals). However, the same result was not repeated for penile responses (measured using a mercury-in-rubber gauge). They also plotted the values of 'male sex film' minus 'female sex film' contrasts for sexual arousal and found a trend for an increase, with diminishing returns, in the value of the contrast with increasing degree of homosexual preference. Overall, they interpret their results in terms of 'bisexuals' consisting, in fact, of individuals with either a homosexual or a heterosexual type of attraction and arousal, and they conclude that 'with respect to sexual arousal and attraction, it remains to be shown that male bisexuality exists' (p. 582). I offer an alternative interpretation of their results.

First, levels of arousal that can cause penile erection may be associated with a single sex at any given time in bisexuals, but the preference may shift from one sex to another through time at different time scales (weeks, months, years). Thus studies of arousal should be also carried out with the temporal dimension in mind, and not only by assuming that bisexuality is just a specific blend of strong homosexual and strong heterosexual inclinations that manifest themselves constantly and to a fixed degree over time (see also Weinberg *et al.* 1994: 44–5 for arguments in favour of bisexuality as a continuum rather than a discrete state). Moreover, their result showing that the level of genital arousal caused by the less arousing sex is nevertheless greater than that caused by the neutral stimulus, also suggests that bisexuality should be studied as a continuum between the two extremes of exclusive homosexuality and exclusive heterosexuality, not as a specific and narrowly defined discrete state. Their values of the male–female sexual arousal contrasts also show a consistent trend to increase with the level of homosexual preference in the participants, again indicating that bisexuality is a continuum of states. They also observed that some individuals who were categorized as homosexuals had male–female sexual arousal contrasts around the 0 region, which to me suggests that, in fact, they were probably bisexuals. The work of Rieger *et al.* (2005) has also recently been criticised by Worthington & Reynolds (2009).

Finally, a recent Finnish study published by Santtila *et al.* (2008) in the journal *Biological Psychology* strongly suggests that the potential for homosexual behaviour, and thus the level of underlying bisexuality, could be quite high in the general population (32.8% for men and 65.4% for women) and it could be genetically heritable. We will see in this book how functional bisexuality is in fact the norm, not the exception, among mammals and birds that engage in same-sex sexual behaviours. We will also see that in humans the level of shift in the individual preference for partners of one sex or another is higher in women than in men. Moreover, I will also argue that the conditions for the evolution and maintenance of bisexuality are far less restrictive than those concerning exclusive homosexuality.

Cross-cultural studies of homosexuality have also produced some interesting generalisations. First, it is clear that homosexuality is found across many human cultures (see, for example, Whitam 1983). Second, focusing on male homosexuality, an early review by Crapo (1995) suggested that three major groupings of male homosexuals exist:

(a) those displaying *intragenerational* homosexuality, where individuals who are engaged in same-sex sexual behaviours are of similar age,
(b) those of the *intergenerational* kind, where the age of the individuals is different and the older participant often takes on a mentorship role towards the younger, and
(c) all the rest.

More recently, Cardoso & Werner (2003, cited in Cardoso 2005) have suggested a different, and in my view better, cross-cultural classification:

(a) *pathic* or *gender-stratified* systems of homosexuality, where males displaying culture-specific traits (usually feminised) have sex with masculinised males, the latter being functionally bisexual in practice, although they tend to self-identify as heterosexuals; this is the most common type of system around the world;
(b) *age-stratified systems*, akin to the *intergenerational* systems described by Crapo (1995); and

(c) *egalitarian* systems where two individuals of the same sex, who self-identify as homosexuals, engage in sexual behaviours with each other. Egalitarian systems are less frequent than the other systems and they seem to have originated mainly among Europeans and people of European descent (Cardoso 2005). Egalitarian systems clearly indicate the independence between sexual orientation and gender role: homosexuals may be feminised, masculinised, androgynous or 'third gender'. Early mentions of a kind of *egalitarian* system are already available in Plato's *Symposium* (Halperin 1990: 268–9).

Gilbert Herdt (1984a) also recognised a specific type of same-sex sexual behaviour called *Ritualised Homosexuality*, which involves 'culturally conventionalized same-sex erotic practices' (Herdt 1984a: ix). Because of the symbolic nature of *Ritualised Homosexuality*, age-stratified systems are referred to in this context as *boy-inseminating rites*. *Ritualised homosexuality* is strongly dependent on cultural transmission for its maintenance. This has been dramatically illustrated by Bruce Knauft (2003: 148) in his study of the Gebusi of Papua New Guinea: 'During the course of 16 years, cohorts of young Gebusi men had gone from actively and proudly practicing sex with other men to apparently not even knowing about it'. From a sexual orientation perspective, *Ritualised Homosexuality* is fully consistent with a bisexual capacity in humans.

With regard to women's homosexuality, it is becoming clear from various cross-cultural studies that women are more plastic than men in terms of their ability to undergo changes in sexual orientation throughout their lifetime (see Diamond 2008a for a recent review). Diamond (2008b) describes women's sexual orientation as more 'fluid' than that of men. I believe that generalisations about any kind of mechanisms purported to explain the maintenance of homosexuality in female and male humans can only be achieved after a sufficient number of cross-cultural studies is carried out. Therefore we will draw from what cross-cultural knowledge is available in order to achieve a better understanding of those mechanisms in the various chapters of this book.

The view that regards homosexuality as 'pathology' was established early on by psychologists such as Krafft-Ebing (1886, see also Hartwich 1951), a view that at the time was opposed by Ulrichs and that I also vehemently reject. At the beginning of the twentieth century Magnus Hirschfeld also rejected the notion of homosexuality being a 'biological degeneration', a notion that in those years would soon give way to very dramatic developments through the application of 'racial hygiene' policies in Germany (Amidon 2008). According to Amidon (2008: 68; see also Brennan & Hegarty 2007) Hirschfeld's books provided a considerable part of the fuel at 'the public Nazi book-burnings of 10 May 1933'. On the other hand, Ellis' book *Sexual Inversion*, published in 1898, was regarded as plainly 'filthy' by the judge in a trial in London against George Bedborough, the secretary of the *Legitimation League*, a group of activists who fought for the legalisation of de facto marriages and the legal recognition of 'illegitimate' children, who had the book on sale. At the trial the judge addressed Bedborough so:

> you might at the outset perhaps have been gulled into the belief that somebody might say that this was a scientific book. But it is impossible for anybody with a head on his shoulders to open the book without seeing that it is a pretence and a sham, and that it is merely entered into for the purpose of selling this filthy publication
>
> (Ellis 1967: 309).

Krafft-Ebing, however, did temper his position with regard to the pathological character of homosexuality later in life, according to Havelock Ellis (1946: 193), and he also produced some remarkable insights in his *Psychopathia Sexualis* that I agree with and further develop in this book (Chapter 4). For instance, he was one of the first to suggest that homosexual behaviour may be what we would now call a neotenic trait. Neoteny is an evolutionary process that involves the slowing down of the rate of development of somatic tissues compared with reproductive tissues.

This process produces descendant species with adult individuals that look like juvenile stages of their ancestor. Havelock Ellis (1946) also mentioned the association of homosexuality with both behavioural and morphological traits reminiscent of 'infantilism', a situation expected from the action of evolutionary neotenic processes.

Specific evolutionary theories aimed at explaining homosexuality were already available in the 1950s, such as George Evelyn Hutchinson's suggestion that recessive alleles determining homosexual behaviour could be maintained by heterozygote advantage (Hutchinson 1959). George C. Williams (1966), on the other hand, suggested that homosexuality is plainly maladaptive. The great sociobiology debate of the 1970s brought an emphasis on kin selection (Trivers 1974; Wilson 1975, 1978) socio-sexual functions of same-sex sexual behaviour (Wilson 1975, 1978; see also Dewar 2003), parental manipulation (Trivers 1974), reciprocal altruism (Trivers 1971), mutualism (Trivers 1971) and sibling rivalry (Trivers 1971). More recently, models based on sexual selection, e.g. female choice for feminised males (Cramer *et al.* 1993; Sprecher *et al.* 1994; Miller 2000; Dewar 2003), reproductive skew (see, for example, Dickemann 1993), sexually antagonistic selection (Gavrilets & Rice 2006; Camperio-Ciani *et al.* 2008a) and sexual segregation (see, for example, Dickemann 1993) have attracted great interest, and even selectively neutralistic views have been also put forward (Vasey 2006a).

As biologists were developing their own ideas about the evolution of homosexuality, sociologists, some psychologists and others were developing their *social constructionist* (also known as *social constructivist*) theories in parallel. Social constructionism had one of its greatest advocates in the French philosopher Michel Foucault (Foucault 1976). Sexuality in general is viewed by Foucault mainly in its socio-sexual context, where language, through discourse and therefore communication, is both a means of exerting power and control over other individuals, what an ethologist would call 'dominance', and also a medium to achieve cooperation. If sexual behaviour is the mean of expression of this process of communication involving relationships of power between two individuals, what it is proximately achieved with it is pleasure. That is, pleasure can be manipulated to achieve control over others, in Foucault's view; conversely, sex may also acquire a function to mediate control of power for the attainment of pleasure. In the words of Eric Anderson (2008: 104): 'Social constructionism attributes the creation of gendered identities to a complex process of cultural, institutional and organizational influences ... alongside individual agency ... with the "power of discourse" ... serving a system of exchange between these systems' (see also De Block & Du Laing 2007 for a concise introduction to social constructionism). DeLamater & Hyde (1998) define what they refer to as the *constructionist paradigm* in the following terms, that I reproduce verbatim except for some slight modifications to adapt them to the specific case of sexuality: (1) Our sexual experience is ordered, (2) language provides the basis on which we make sense of that sexual experience, (3) the reality of sexual life is shared, (4) shared typifications of sexual life become institutionalised, and finally (5) sexual knowledge may be institutionalised at the level of society, or within groups. The so called *Ecological Theory* is a recent derivation of social constructionism that seeks explanations of sexual behaviour at three different levels: the individual level (microsystem), the level of immediate interindividual relationships (mesosystem) and that of broader relationships within the community at large (exosystem) (see, for example, Henderson *et al.* 2008). Applications of social constructionist views to the understanding of homosexual behaviour, that rely on the action of learning mechanisms, can also be found in Storms (1981), Tyler (1984), Hogben & Byrne (1998), Ågmo & Ellingsen (2003) and Anderson (2008). We will see how social interactions and (to a variable extent) learning are very important, but by no means the only, causative explanations of homosexual behaviours.

Psychoanalytical theories that are inspired by Sigmund Freud's works (e.g. 1905, 1919, 1931) are