

An association between male homosexuality and reproductive success

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Summary The existence of homosexuality in humans poses a problem for evolutionary theory. Exclusive male homosexuality has a catastrophic effect on reproduction and yet inherited factors appear to contribute to it. Previous attempts to resolve this conundrum are inconsistent with aspects of evolutionary theory. Additional limitations are as follows. Until recently, accounts of homosexuality have paid little attention to the probable existence of adaptive bisexuality in ancestral populations, from which further variations in sexual orientation may have evolved. Secondly, previous explanations have concentrated on the ancestral environment of two to three million years ago as the determinant of modern sexuality, when more recent influences are likely to have had considerable impact. I argue in favour of a longitudinal rather than cross-sectional model of the ancestral environment. Thirdly, they have often ignored the possibility of variable phenotypic expression, whereby those individuals with a genetic propensity for homosexuality exhibit different and adaptive qualities on most other occasions. It has been demonstrated in previous studies that homosexual men have superior linguistic skills compared to heterosexual men. This may be the result of an adaptive feminising effect on the male brain and apply to many practising heterosexuals. Other adaptations to the recent ancestral environment may include enhanced empathy, fine motor skills and impulse control. By drawing together these contributing factors an evolutionary basis for homosexuality can be demonstrated.

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INTRODUCTION

Whilst evolutionary theory explains many puzzling aspects of our condition it also highlights others that become puzzling when viewed from the evolutionary perspective (1). One of these is the existence of homosexuality in humans (2–4). It is thought that 3–10% of men and 1–4% of women are exclusively homosexual (5). If an individual is exclusively homosexual it is unlikely that they will leave any descendants. Yet homosexuality in humans appears to have an inherited

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Correspondence to: **Colin S. Dewar** MRC Psych., Kildean Day Hospital, Drip Road, Stirling FK8 1RW, UK; E-mail: colin.dewar@fvpc.scot.nhs.uk component (6–8). All homosexuals are descended from heterosexual predecessors. The puzzle then is to suggest a mechanism whereby such genes that block reproduction have proliferated in the population.

In this article, I will summarise environmental contributions to homosexuality as part of a multifactorial model. For the purposes of brevity I will not review previous explanations for the environmental contribution to homosexuality as they are covered elsewhere in the literature.

I intend to focus on male homosexuality. Both male and female homosexuality are equally significant from the sociological perspective, but the evidence suggests that they have different genetic aetiologies (6,9,10) and so the explanations for them may be different. If this is the case it may be unnecessary to encompass both in a single explanation.

ACKNOWLEDGING THE NEED FOR A MULTIFACTORIAL MODEL AT THE OUTSET

Since genes are not the only determinant of sexual orientation, a multifactorial model is needed. Recent accounts of sexuality have suggested that many influences are at work, combining nature and nurture (7,8,11). A simplistic account is that we inherit a propensity towards a certain sexual orientation, that this may be subject to a delayed influence during early development through parenting according to a psychodynamic model (12,13) and then further modified by social learning during development and by formative sexual experiences as we go through life (14,15). As time passes each superimposes on the last.

THE SIGNIFICANCE OF BISEXUALITY

Homosexuality need not be confined to obligatory homosexuals. People can be actively bisexual throughout life (16), or experiment with homosexual encounters in adolescence and become heterosexual as adults (17) or heterosexuals can resort to homosexuality in single sex environments (18), or practising heterosexuals may harbour homosexual desires which they are unwilling to enact (19). One could argue that all humans are potentially bisexual (5) and that we confuse the issue when we concentrate on sexual orientation as a discrete category rather than on sexual behaviour as a flexible phenomenon (4). The extent to which either propensity is developed may be influenced by social circumstances.

Homosexuality as an adjunct to heterosexuality may have assisted survival and reproduction for millions of years. Once homosexuality is seen as sinless it is possible to consider a range of benefits. If opportunistic homosexuality is enjoyed alongside heterosexuality by most population members, as just one type of social interaction, then it can function as a means as enforcing friendships, just as grooming serves this function in many primates.

It is notable that bonobos, our near kin, exhibit bisexuality (though apparently not exclusive homosexuality). Similarly, boys in ancient Greece sometimes pleased men with sexual stimulation. Sexual impulses like any evolved phenomena may be subverted for other purposes (20).

Grooming, massage, and sexual contact at an animal level are not such different things. It is thought to be the case that friendships form in social animals for mutual exchange of resources in the short term and co-operative alliances improving mating opportunities in the long term (20). Any sexual contact that promotes this process, preferably in forming an uneven alliance in favour of the protagonist, is likely to prove adaptive. There is a well-established tradition of human females exchanging sex for resources or social promotion but if homosexuality was widespread then the same could occur with members of the same sex. Once homosexual contact with the appropriate person was established then opportunities for heterosexual contact and the proliferation of genes could continue at a higher level. Reproductive benefits might be indirect (status and access to resources) or direct (access to shared mates).

On writing this article, I have learned that this mode of explanation and supporting evidence has recently been published (21,22).

According to popular wisdom, in every small man, there is a big man waiting to come out. Is it the case that in every heterosexual there is a homosexual waiting to come out, and vice versa, according to circumstance? Information from primate studies suggests that this is the case, (22) but information from contemporary human society does not. Whilst there does seem to be a continuum between homo and heterosexuality with an extensive grey area in between, the existence of this grey area should not prevent us from being clear headed about the extremes at either end. Some homosexual men strive to be heterosexual without success. Eventually they accept homosexuality and thereafter effortlessly disregard members of the opposite sex as possible sex objects. Whilst committed heterosexuals in single sex environments, can be dismissed as the product of social conditioning, it is more difficult to dismiss the experience of obligatory homosexuals. They have already overcome social stigma to live as they do. It would provide little additional social stress to switch to the bisexual subculture if they were so inclined.

In other primates, and in early human societies in most cases, homosexuality appears to have been a precursor to heterosexual reproduction (or at least not to have hindered it). A male silverback gorilla in an all male group may tolerate the sexual advances of a younger male (21) but we do not see two dominant adult silverbacks departing into the jungle for lifelong intimacy when there is an harem of females freely available. Yet equivalent liaisons appear to occur in modern human society.

This theory has the curious feature of making the bisexual male more akin to the exclusively heterosexual male in evolutionary terms (though not in psychological terms). Homosexual behaviour gains meaning in terms of its eventual contribution to heterosexual reproduction. It is validated as an evolved strategy by the heterosexual behaviour that becomes possible as a result. The reverse does not apply. Homosexual reproduction does not occur in humans and so opportunistic heterosexual behaviour in a predominantly homosexual male cannot be accorded the same evolutionary status as its counterpart in the heterosexual male. In this article I will therefore use the labels hetero and homosexual as convenient but incomplete expressions of the complex bisexuality that often underlies them. The first refers to behaviours that are likely to increase progeny as an end product and the second to behaviours that are not.

One advantage of the alliance theory of homosexuality is that it could account for homosexual activity at any time in history. Another is that it could also help to explain female homosexuality.

The main disadvantage is that it does not fully explain exclusive homosexuality. Something else is needed.

THE NEED TO TAKE INTO ACCOUNT EVOLUTIONARY FORCES FROM DIFFERENT TIMES IN HISTORY: A LONGITUDINAL RATHER THAN CROSS-SECTIONAL VIEW

Previous evolutionary accounts of male homosexuality have taken the environment of two to three million years ago as the determinant of human sexuality (3). However much of Europe and Asia has existed for many thousand years outwith a Stone Age environment. As society and sexuality are interlinked, this extensive post-Palaeolithic period is likely to have had a profound impact on the genes required for adaptive sexual expression. My hypothesis is that modern sexual expression and in particular homosexuality in men may owe much to post-Palaeolithic influences.

OVERVIEW OF FACTORS AFFECTING THE DIRECTION OF HUMAN EVOLUTION

One of the problems facing the evolutionary perspective is that we cannot be sure which part of our evolution explains current phenomena. It is a bit like trying to find our geographical roots, in order to attach ourselves to a particular culture, only to find that our ancestors were always on the move. Evolution does not progress in straight lines. The ancestors of seals lived in the sea and then they lived on land and now they live in the sea again. Is the seal evolved from a sea or a land animal? Man is a tropical animal but some groups are adapted to life in the Arctic. Hence we can expect to find recent adaptations superimposed on a contrary underlying design.

What is surprising is that Evolutionary Psychology is focused on the hunter–gatherer (or foraging) period in our existence as though nothing much is likely to have happened thereafter. Our evolution is described as if the pressures influencing it were the same at all times, and the ancestral environment of two to three million years ago as the one and only ancestral environment. In fact we have innumerable, linked ancestral environments all the way from the beginning of life on Earth to the time of our own conception, depending on the quality that is being studied.

That is why I must now make an effort to demonstrate that evolutionary forces often change direction.

If we apply ourselves to factors driving the evolution of human psychology we are faced with a staggering series of transitions. Even if we confine ourselves to the last three million years, when intelligence must have played a major part in our differential survival we have evolved through a number of contrary cultural trends (23).

Evolution does not proceed at the same rate at all times. So longer rather than shorter periods of time are not in themselves cause to think that we became more evolved during them. Our two million years as huntergatherers when the human brain evolved to its current size may be more important than another two million years when we changed very little. And within those two million years of rapid development, some millennia may have been more important than others.

In general evolution proceeds more quickly when there is a change in lifestyle, for example as a result of a change in the environment. Another determinant is that ancient structures such as our skeleton are likely to be committed to a certain form at an early stage in evolution and to undergo only superficial change thereafter, whilst modern structures like the neocortex of the human brain are much more likely to be susceptible to modern evolutionary effects. So for example the inherited components that affect the way in which we use language are more likely to be more heavily influenced by selective pressures over the last two million years than by selective pressures over a similar period of time during the amphibian stage of our evolution. Extrapolating this argument the most recent may have been the most important of all.

If a period of time is sufficient to conclude an adaptation that reverses a previous adaptation, then it is the most recent selective pressure that will be manifested through the phenotype. This applies regardless of the many millennia in which the original adaptation held sway. In humans, new selective pressures appeared to varying extents in different parts of the world over the last 10,000 years (23).

How long do we need for evolutionary change to take place? Various examples indicate that it can occur fairly quickly. Only 100,000 years ago the distinction between the races as we know them today did not exist (24). We were all of African stock. The subsequent differentiation between occidental and oriental groups is likely to have arisen even more recently than that and the differentiation between for example Northern and Southern European groups yet more recently still. Regional tolerances to cow's milk match those where cattle have been kept for thousands of years and probably evolved since the domestication of cattle (25,26). In other animals there are much faster examples of change, even once we have taken into account the shorter life cycle. Through artificial selection, most varieties of modern dogs have been bred in just a few hundred years.

Rapid genetic change is likely to occur if there is a founder effect (when a subsidiary population is descended from a single individual) or during catastrophes when most members of a population die, or if polygynous mating system is in operation. If all the females mate with just a few males and if a beneficial change occurs in one male, increasing his reproductive success, then those genes will spread through the population very rapidly. In human societies polygynous mating became more common after the introduction of agriculture (3). If any of these factors apply a significant genetic shift could occur in just one generation.

Genetic shifts are at the root of evolutionary change. This applies whether the new morphology arises from dimensional or categorical change. In the latter case an evolutionary change could occur very rapidly if certain environmental conditions applied. But even without categorical change, a slower dimensional change with the mean point of a normal distribution creeping up gradually from one generation to the next could effect a similar change in due course. It need not take tens of thousands of years and certainly not millions of years. Millions of years are needed for the really big changes, like the formation of new types of animal.

TOWARDS AN ALTERNATIVE EXPLANATION FOR HOMOSEXUALITY. A WIDER PATTERN OF GENETIC ACTIVITY IS LIKELY

If homosexuality is a naturally selected feature within the population then it may be just the tip of the iceberg. Since other simpler explanations have proved insufficient I have to consider the possibility that homosexuality represents a wider pattern of genetic activity. The genes that cause it must be associated with something different and beneficial most of the time. Indeed they could be conceived, not as genes for homosexuality but as genes for something else (2). Such an effect may be active throughout the population regardless of any existing homosexuals. We need to postulate a reproductive benefit as widespread as this to compensate for the catastrophic effects on reproduction arising from exclusive homosexuality.

One starting point is to establish the qualities that would allow a human male to mate successfully with more females. It depends on lifestyle. We can be pretty sure it would not be the same today as those that applied when the human male was a hunter. I talk about males as though females must have been passive observers of the genetic shifts occurring around them. This is only because I believe that the lifestyle of women has changed less than men until the 1950s. Men either hunted or worked in a field or a factory, whilst women stayed behind and gathered and looked after the children. I am not saying that this a desirable state of affairs. History merely records it as an uncomfortable fact.

Men have been under uneven selective pressures. What must have counted when men were hunters was success in the hunt. Competence with projectile weapons and a keen eye for the habits of prey species would then have given any man an advantage over his colleagues. Physical combat with other males from the same or other groups may also have been a frequent feature. He needed to be able to act quickly and decisively. He would thereby have more meat, have high social status and be sought after by women as the progenitor and perhaps provider for their children.

What happened when agriculture became the new modus vivendi as it did in some parts of the world over 10,000 years ago? Men still required good visual-spatial skills, though modified in type, but now needed all sorts of other skills, hitherto the prerogative of women. Trades became possible, requiring enhanced social skills. Expertise in a difficult activity, required by the remainder of the population, must have promoted social status. The larger social groups in which people lived must have meant more social contact, and no trivial contact at that. In the absence of any welfare state the quality of our relationships with other people would have had a profound impact on our social status, and perhaps survival. It might now have been necessary for us to evaluate and remember the personalities of a thousand people, an area of functioning in which women usually exceed men. Deception, fraud and other manipulative behaviour would for the first time have been commonplace. These require excellent interpersonal skills. In a hunter-gatherer population, manipulation would always have happened but group numbers would have been smaller, everyone would have known each other and the degree of genetic kinship would have been greater (thus lessening the genetic advantage that would accrue to fraudsters). Reputation is guarded in inverse proportion to the size of the community (20).

With the arrival of agriculture, human males were suddenly under a different type of selective pressure. Females were too but to a lesser extent. Their success or failure had always been domestically based. Males now needed better interpersonal skills and more patience to deal with repetitive tasks. If you cannot talk to people you cannot persuade them to do things for you. It is likely that successful men have always used alliances to help them to achieve their goals, just as chimpanzees do today. It just became more important when our species settled in large, permanent communities.

Circumstances only got worse for hunting men as civilisation developed further. Once education became related to success, hunting qualities became maladaptive. Sitting in a school classroom and studying in the evening is almost the opposite of killing wild boars with a spear. Academics do not need to be combative, impulsive and predatory. In fact these qualities would be disadvantages. Men who lead from the front may do well in small groups but in modern times it may be better to lead from the back and this requires a different type of person. With the passage of time the aptitude for language that this requires has become increasingly important.

Success in studying or carefully planning and persisting with business projects (which utilises similar skills) became the gateway to success. Such men could amass wealth and we know from history that wealthy men left more descendants. They could buy bodyguards or 'helpers' of whatever kind. Wealth, social status and the sexual desirability of men go together even now (26). Impulsive individuals with poor social and academic skills may have resorted to crime. If discovered this led to imprisonment or death, both of which were likely to curtail reproductive success.

MEDIATORS OF MASCULINITY

In times of peace, those who go along get along. People who work hard and co-operate do better in the long run on average under modern conditions. They put themselves in the best position for promotion at work. It is only in films that the improbable hero against impossible odds wins the day.

In times of global war, cautious and intelligent people who manage to stay away from the front are more likely to survive than those who do not and are well placed to reproduce afterwards once the competition has been thinned out. (The moral status of this strategy can be ignored from the evolutionary perspective.) For the individual the benefits of large scale, internecine war are much reduced from those applying to small-scale tribal conflict, while the risks may be the similar.

As a result of changes in society following the discovery of agriculture, and more so in the industrial era, human males needed more feminine skills. What would be an easy way for evolution to bring this about? Masculinity is mediated through androgens such as testosterone. Under such conditions, relative androgen resistance would be an asset for any man. He would have improved impulse control (reducing the likelihood of random violence, death during mass war and conflict with important figures in the community during times of peace) and at the same time the improved social awareness and communication skills of women. He might also have enhanced fine motor skills, crucial for certain trades and preferentially associated with women (27). All of these would be likely to enhance survival. Whilst the literature indicates that differences in function between homo and heterosexual males may not be marked the cumulative effect of many small advantages could lead to a significant adaptive effect.

Androgen insensitivity in regard to its possible relationship to homosexuality has already been discussed in the literature (7).

There is evidence that the brains of homosexual men function differently from the brains of heterosexual men (28–35). It is not just sexual orientation that distinguishes homo and heterosexual men. Whilst not an invariable association, most studies comparing homosexual men, heterosexual men and women have indicated that homosexual men are more like women in their intellectual function than heterosexual men (30–35). They have superior verbal abilities compared to heterosexual men (31,36,37). As far as I am aware the relatives of homosexual men have not been subject to this kind of study.

Since it is too simplistic to explain mental and sexual function in terms of androgens I must emphasise that when I use the term 'androgen resistance' I mean it only as a temporary but convenient label for selective influences on parts of the male brain so far poorly understood. It does not matter which way it is formulated. Heterosexuality could likewise be 'explained' as an inherited sensitivity to these same influences.

One means of looking for evidence for or against this theory would be through assessment of groups of people who have had little or no contact with the modern world (but not their descendants after that contact). We do not have much information about the sexual practices of pre-agricultural groups, but what little there is indicates that homosexuality, when it occurred, was not an exclusive phenomenon but fulfilled a social role alongside widespread heterosexual activity (17,38–40).

From the study of other mammals a similar pattern emerges. Bisexuality is common in social mammals but exclusive homosexuality, if it exists, is extremely rare (41).

Exclusive homosexuality is difficult to explain from an individual perspective because it limits progeny to such an extent. However if we see it as being at one end of the population spectrum in terms of androgen resistance then it makes sense. A balanced polymorphism may exist in which beneficial feminising effects offset the adverse effects on reproduction that may arise from homosexuality (42).

I still need to explain why genes for moderate androgen resistance in males as the preferred optimum (associated with heterosexuality and good social and communication skills) would not replace all other types of gene. For this I need to refer to orthodox genetic theory. Androgen resistance is unlikely to be an all or nothing effect. In any normally distributed population there may be a few individuals who are very androgen resistant and a few that are very androgen sensitive. Either may be at a disadvantage in terms of reproductive potential, but will continue to appear in the population. It is the selected mean which determines the probability that certain deviations from the mean will occur. I believe that the optimum degree of androgenism (or other proxy for masculinity) has shifted due to changes in lifestyle over the last 10,000 years.

FURTHER DEVELOPMENT OF THE THEORY

It also needs to be borne in mind that even for androgen resistant men the die is not cast in terms of their sexuality until after birth. Otherwise identical twins would have identical sexual orientation as adults, which is only true about half the time (3). Environmental factors have a significant impact. So it could be formulated as a kind of gamble. According to this theory a male foetus is conceived with genes that are probably going to be very advantageous but if certain environmental conditions prevail, either before or after birth, then he develops a homosexual orientation. Modern environmental conditions may or may not increase this risk. This is a subtle development of the preceding explanation, which uses graded departure from the mean of a normal distribution as the preferred explanation. This is now saying that even the majority of the male population might be prone to homosexuality but that the environmental triggers fail to occur for most. Another example of this kind of effect is large head size in human infants associated with infant mortality. Throughout evolution large brain size has been selected because of its positive association with intelligence, but this large brain size kills a small number of offspring at birth because they cannot get through the birth canal. We all have large heads but only a small number of us die at birth and it is difficult to say in advance which foetuses will die at birth because of their head size. Other factors come into it.

Death at birth in a small percentage, say 5% under natural conditions, might be akin to the reproductive catastrophe of exclusive homosexuality. Neither the dead infant or the homosexual is likely to reproduce and so one would expect the genes associated with them to be edited out of the gene pool fairly quickly. However they aren't edited out because both sets of genes make so much difference the rest of the time in the remainder of the population. It might be safer at birth to have a small head with a small brain and to be born with the ease of a puppy but it is just too massive a disadvantage throughout the remainder of life. In reproductive terms it's better to take the risk associated with a large head. Similarly it might be too big a disadvantage in a post-hunter-gatherer society to be aggressive with poor communication and social skills (as a result of being highly responsive to available androgens) even if the alternative means there is a 5% chance of being exclusively homosexual. This also parallels the observation that homosexual children are born to heterosexual parents. Parents with large heads who have survived childbirth may themselves conceive children who do not. Indeed it is invariably the case that parents of children who die during childbirth survived their own birth.

SYNTHESIS OF CONTRIBUTING FACTORS AND CONCLUSION

It is time to draw together an account of how different evolutionary factors may have interacted. If we go far enough back in time it is likely that opportunistic homosexual activity may have supported heterosexual activity by fostering alliances. The evidence for this is firstly that we often find opportunistic homosexuality in social animals, where it appears to contribute to social function, but we do not find exclusive homosexual activity. Secondly what little we know about sexuality in remote tribes prior to contact with the modern world indicates that homosexual activity was subservient to social function. It was associated with rituals and social bonding. Whilst it may have been pleasurable in itself, it does not seem to have been the sole mode of sexual expression. Participants appear to have operated heterosexually on other occasions.

I think that as a species we probably arrived at the agricultural era with the bisexual behaviour exhibited by other social animals. It may have remained adaptive thereafter (because of its association with success within male groups). However additional selective pressures came into operation after the adoption of agriculture and working on variations in social and linguistic skills these pressures gave rise to further evolution. As a by-product this was associated with exclusive homosexuality in a few individuals. Men were at a reproductive advantage if their social and linguistic skills were above average. Research on homosexual men in the modern era indicates that they have linguistic function that is above average for men. They may also have other aptitudes, characteristically associated with femininity, and be more inclined to co-operate rather than compete with other members of the population. A high level of aggression, once adaptive, is likely to prove maladaptive in large communities.

Furthermore if there were people with a predominantly homosexual orientation, social conditions probably limited its expression throughout much of recent history. In our era homosexual people have a subculture but in the past I suspect that many homosexual men (by which I mean men who would be exclusively homosexual given the choice) simply got married and had children. Social factors may have been inhibitory. Even in this era many homosexual men have been or are married (8,30).

It is evident from this and other accounts that no single explanation for human sexuality is sufficient (21). Male homosexual behaviour is weakly correlated with numerous factors, but even if there are numerous contributory factors, this need not prevent us from trying to elucidate them one by one and to dismiss any that seem to be erroneous. I hope in this article to have contributed to this task.

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