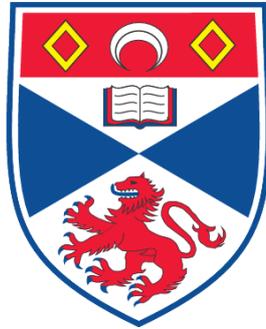


**THE EFFECTS OF PUBERTAL TIMING AND DOMINANCE ON
THE MATING STRATEGY, APPEARANCE AND BEHAVIOUR OF
MEN**

Jamie F. Lawson

**A Thesis Submitted for the Degree of PhD
at the
University of St. Andrews**



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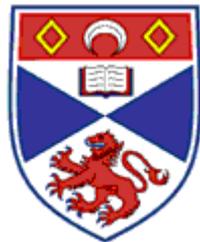
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THE EFFECTS OF PUBERTAL TIMING AND DOMINANCE ON THE MATING STRATEGY, APPEARANCE AND BEHAVIOUR OF MEN.

JAMIE F LAWSON



University of St Andrews

This thesis was submitted for the degree of Doctor of Philosophy in
October 2007

I, Jamie Fletcher Lawson, hereby certify that this thesis, which is approximately 41, 000 words in length, has been written by me, that is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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Acknowledgments

The work presented here would not have been possible without the invaluable assistance and guidance of my supervisor, David Perrett, and the support and help of my friends and colleagues (past and present) in the Perception Lab: Michael Stirrat, Miriam Law Smith, Ian Stephen, Janek Lobmaier, Johannes Schindelin, Vinet Coetzee and Elizabeth Cornwell. Specific thanks must go to my examiners, Andrew Whiten and Robin Dunbar, for a stimulating and enjoyable viva. I am grateful also for the input of Simon Townsend into this thesis and for the friendship and support of my fellow PhD students in the School of Psychology.

Further thanks to Bernard Tiddeman for the technical magic of Psychomorph, to Anne Perrett for proof-reading and to Lesley Ferrier for scheduling participants and generally keeping me sane. Thanks to Martin Sharp and Emad Al-Dujaili for the hormone analysis and to Mary Latimer for helping me spin down spit on more than one occasion. Thank you to Lisa DeBruine for assistance with the BBC dataset and with further software and programming help. Thank you to the BBC for giving me access to such a huge quantity of data. Thank you to anyone who had their photo taken, told me about their sex-life or spat in a bottle in the name of science. Thanks also to Tom, Khalil, Olga, Elaine, Cat, Shehnaz and the other undergraduate project students who assisted with data gathering.

Finally, thank you to all my friends, family and flatmates for listening me talk about puberty and dominance for so long without complaining, thanks to David Bowie and Queen for 'Under Pressure' and thanks to John Hayton for turning up just in time.



This work is supported by a BBSRC grant and by Unilever

Note to the reader:

Throughout all of the experimental chapters in this thesis, I have used the pronoun ‘we’ as opposed to ‘I’. The work herein is unequivocally my own in terms of hypotheses, analyses and conclusions. The Perception Lab is an inherently collaborative environment and all members assist in the running of participants, the taking of photographs, the setting up of software and experiments, the pooling of questions and data and the exchanging of ideas. Such collaborative effort must be acknowledged. Additionally, many of the experiments described within this thesis were run as part of a larger group of experiments, pooling participants for maximum efficiency. The plural pronoun reflects the fact that, if published, the experiments within would carry multiple authorship and is used in keeping with intellectual honesty.

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Abstract

Pubertal timing is a human life history variable representing a trade-off between early reproduction and continued growth. Dominance is an important feature to male mate value. These two variables should have far-reaching effects on adult male life. Chapter 1 reviews evolution, r/K selection and life history theory to derive hypotheses concerning variation in male mating strategy. Chapters 2-4 investigate the effects of pubertal timing and dominance on mating strategy using sociosexual orientation and preferences for faces and mate characteristics. Both early puberty and high dominance associate with unrestricted sociosexuality (increased interest in casual sex) as predicted. Dominance is shown to relate to preferences for cues of sociosexuality but not femininity, while pubertal timing relates to neither facial characteristic. Earlier and later developing men do not differ in their mate characteristic preferences, while dominant men exhibit enhanced female-typical mate preferences counter to predictions. A dominance-dependent, dual, male mating strategy is proposed to account for results. Chapter 5 introduces sensitivity to putative human pheromones as an indicator of mating strategy. Dominant men are found to be more sensitive to and more averse to a putative female pheromone. Pubertal timing has no effect on sensitivity. Results are interpreted in terms of dominant male avoidance of infertile matings.

Chapter 6 finds that early puberty associates with facial masculinity, attractiveness and apparent age. Chapter 7 offers a hormonal underpinning of effects related to pubertal timing, showing that early development associates with higher levels of testosterone in men. Chapter 8 uses digit length ratios to show that early developing men may have been exposed to greater levels of uterine testosterone, suggesting prenatal influences on male pubertal timing. Chapter 9 shows dominance associates with bodily, vocal and general attractiveness but not facial attractiveness. Chapter 10 reports that dominance associates with high levels of the stress hormone cortisol, suggesting costs

of high dominance. Chapter 11 shows early pubertal timing relates to the visual appearance of skin, perhaps because of lower sebum production among early developing men, leading to them having darker, less reflective skin. This may reflect accelerated ageing of early developing males, potentially representing a cost to longevity.

1 Introduction: evolution, r/K selection, life history theory, puberty and dominance.

1.1 Introduction

This thesis investigates the effects both age at puberty and dominance on the appearance, hormone levels and behaviour of men. A central premise of the arguments presented here is that humans have faced selective pressure over our evolutionary history towards the optimal allocation of energy and resources to reproductive and personal growth events, and, as a species of hominoid primate, use information on our own individual social dominance to inform on reproductive decisions. Both of these hypotheses rely on the theories of natural and sexual selection. Before continuing to outline the basis of the specific hypotheses within this thesis, it is first necessary to present a brief summary of contemporary evolutionary theory.

1.2 Evolution

Evolution, as a biological phenomenon, is the process of change over time of traits possessed by a species or lineage of organisms (Darwin 1859). Evolutionary mechanisms operate through competition between individuals and lead groups of organisms to become adapted to (i.e. good at making a living and surviving in) their environments (Ridley 2004)

Modern evolutionary theory is based on the works of Charles Darwin who generated theories of evolution by natural and sexual selection based on observations made during his voyages on the HMS Beagle (Darwin 1859). The theory was born of two main observations: that otherwise similar forms in the same area may differ in some features if they are exploiting different environment; and that similar environments produce similar features in species in different parts of the world. Darwin noted that there are vastly fewer organisms in any species than would be predicted if all individuals

who were born survived and if all individuals were reproducing; that offspring tend to resemble their parents; and that there tends to be variation of traits within groups of organisms (Darwin 1859). Variation of traits means that some individuals may be better than others at accessing resources or at surviving predation in the local environment and may thereby be more likely to survive and to pass their beneficial or advantageous trait on to their offspring. The basic principles of differential survival, heredity and variation lead inevitably to a steady increase in fitness (a mark of evolutionary success) within a population and to morphological change leading, ultimately, to novel forms which are well adapted to their environment. After a long enough accumulation of small modifications, the organism becomes sufficiently different from its starting point to become a new species, a phenomenon called speciation (Darwin 1859; Dawkins 2005). The processes of selection and speciation as defined by Charles Darwin provide us with a mechanism for the adaptation of living organisms to their environment.

Darwin himself was unaware of the existence of genes or of any physical mechanism for the inheritance of traits through generations. The re-discovery of the works of 19th century Austrian monk, Gregor Mendel (Mendel, 1859) and the development of modern genetics provided a source of variation on which for evolutionary selection to act. Modern evolutionary theory is based on competition between individual genes and alleles for inheritance the next generation (Dawkins 1979; Ridley 2004). Selfish gene theory (Dawkins 1979) formalised these ideas and placed competition between genes at the centre of evolutionary processes. Put simply; genes which promote their own expression in the next generation through, for example, generating survival or reproduction enhancing phenotypes will be more likely to occur in the next generation owing to the higher likelihood of reproduction for the individual who possesses them.

1.2.1 Natural selection

The process of gamete formation by cellular meiosis and recombination leads to novel combinations of parental genes. This means that, although offspring share genetic material with their parents, different combinations of genes may be expressed. This leads to variation in phenotypes within and between generations (Ridley 2004). In each generation, the individual organisms whose phenotypes are best suited to their environment are more likely than others to survive long enough to reproduce, thereby passing on their genes to the next generation, causing the advantageous phenotypic traits to spread through a population and the deleterious or disadvantageous traits to be steadily selected out. The process of natural selection is driven by the action of the environment on individual organisms and causes changes to emerge in the morphology of species (Dawkins 1979; Dawkins 1986; Jones 1999; Ridley 2004).

1.2.2 Evolution of Behaviour

Theories of evolution by natural selection are readily applicable to any trait of an organism that has a genetic basis. Although theories exist to account for non-genetic selection (for example, meme theory, (Dawkins 1979; Laland & Brown 2002) , natural selection requires that a central unit of information is replicated and transmitted through generations. While genes were an unknown phenomenon to Darwin, modern genetics has exposed a clear source of variation on which selection can operate. As a summary of modern evolutionary theory: selection operates on the genotype of a species through the interaction of individual phenotypes with the environment (Jones 1999; Ridley 2004).

The phenotype of an organism does not by any means exclude its behaviour. In fact, the suite of behaviours operated by an organism to make a living are prime mechanisms by which an individual

can interact with its environment. As such, behaviour is a readily selectable trait *insofar as* it has a genetic basis (Laland & Brown 2002; Sokolowski 2001). While the extent to which different behaviours are genetically based rather than acquired through learning and experience (noting that a learned behaviour may also have a genetic basis (Phillips et al. 1998) is debatable, it is clear that *if* genetic variation for a behavioural trait exists then behavioural phenotypes that enhance the spread of the genes which influence them will spread through a population (Dawkins 1979; Dawkins 1986). Since behaviours related to food acquisition, predator avoidance and reproduction are crucial to survival and fitness, they are highly likely to have been subject to selection. This thesis assumes that mating behaviours have some genetic basis and have been shaped by selective pressure over evolutionary time.

1.2.3 Sexual selection.

The first chapters of this thesis are concerned with human mating strategy and attractiveness. Reproductively relevant traits such as these are prime targets for selection, since successful reproduction is at the core of any evolutionary process. Any trait that promotes the spread of an individual's genes in the next generation leads to selection for and the spread of that trait within a population. Traits which enhance the likelihood of successful and frequent mating are clear candidates for selection (Andersson 1991; Miller 2000; Ridley 2004). While natural selection is the result of an individual interacting with its environment, sexual selection is mediated by other members of the individual's species, as long as that species reproduces sexually. Sexual selection has two components; competition for mates between members of the same sex, *intrasexual selection*, which can lead to the evolution of weaponry or large body size, and the exploitation of preferences and sensory apparatus of the opposite sex, *intersexual selection*, which tends to promote the evolution of ornaments and behavioural displays (Andersson 1991; Ridley 2004; Wich et al. 2004).

The processes of inter- and intrasexual selection lead to the spread of attractive traits through a population, as long as those traits have a genetic origin. There are alternative theories addressing the reasons for which a trait becomes attractive. Good-genes sexual selection theory (Hamilton & Zuk 1982; Moller 1999; Trivers 1972; Zahavi 1975) holds that attractive traits signal the genetic quality of the individual. For example, a colourful, brilliant, symmetrical peacock's tail may indicate that the peacock has a healthy immune system capable of defending the male bird from parasites and pathogens that would otherwise dull the colours or disturb its ontogenetic trajectory towards symmetry and is attractive because of the genetic benefits mating with such a male would bring to offspring (Andersson 1991; Moller 1999). Alternatively, the Handicap Hypothesis states that attractive traits signal the ability of an individual to survive and remain healthy despite a costly ornament (Folstad & Karter 1992; Wedekind & Folstad 1994). Here, the peacock is advertising a diversion of resources that would otherwise be invested in immune system functionality in to the growth of a bright tail, thereby indicating his ability to survive in spite of an impaired immune system which must, therefore, be extremely strong and, following similar logic, attractive owing to the heritability of the immune system. A third option is that attractive traits remain attractive because they have attracted mates. To clarify the tautology; a peahen may be attracted to the peacock's tail because it has hijacked and exploited an aspect of her visual system. Since females are attracted to this trait, it is in a peahen's interest to ensure that male offspring have this trait in order to enhance the reproductive success of her sons; the Sexy-Son Hypothesis (Weatherhead & Robertson 1979), but see Kirkpatrick (1984). It should be noted that these three theories are not necessarily incompatible.

1.3 Facial Attractiveness

Cross cultural research in to human attractiveness suggests that different human groups show a great deal of homogeneity in their judgments of attractiveness. This is grounds to hypothesise that there are species level adaptations within the human mate choice arena. Facial averageness, facial

symmetry and facial masculinity (or femininity) have consistently been shown to be important features to facial attractiveness. Since this thesis is concerned to some extent with facial appearance (Chapters 3 and 6), a brief review of these ideas is appropriate.

1.3.1 Facial Averageness

Facial averageness was first identified as an attractive feature in the 19th Century by Francis Galton. While attempting to create a prototypical criminal face by blending the images of convicts, Galton discovered that adding more faces to the resulting composite increased the attractiveness of the image. More recent work by Benson & Perrett (1992; Little & Hancock 2002; Penton-Voak & Perrett 2000; Perrett et al. 1994), using computers to create average faces from groups of individuals, have shown that facial composites are routinely more attractive than any of the constituent faces. Consequently, individuals who more closely resemble the average for their group are more attractive. Two main explanations have been proposed for this phenomenon; Symons (1979) suggests that natural selection pushes facial features towards the mean configuration because people with average features are better at essential tasks like chewing or breathing. Consequently, average features advertise good (i.e. well adapted) phenotypic condition. Thornhill and Gangestad (1999) suggest that facial averageness signals high levels of protein heterozygosity, providing effective resistance to parasites. Both of these possibilities would give an averagely featured individual high mate value owing to the potential genetic benefits they could provide to offspring. Langlois et al. (Alley & Cunningham 1991; 1994) report, however, that facial composites become more attractive due to the smoothing effect on the skin that the process of averaging can have and is, consequently, artificial. Further work has shown, however, that the effect of average face shape increases attractiveness over and above the effect of skin texture (Rhodes & Tremewan 1996).

1.3.2 Facial Symmetry

Similarly, facial symmetry has been associated with genetic quality. Most vertebrates develop during gestation along a bilaterally symmetrical body plan. Deviations from symmetry may

represent the inability of an individual to overcome successfully environmental insults that may otherwise interrupt the process of symmetrical development. Such insults may originate from pathogens, parasites, deleterious mutations or, in the case of placental mammals, the maternal immune system. Ability to overcome these assaults is dependent on the foetal immune system. Therefore, deviations from symmetry are signals of immune system quality (Palmer & Strobeck 2003). Since immune system functionality is substantially heritable, individuals should prefer to mate with symmetrical individuals to benefit their offspring (good genes selection hypothesis (Kodric-Brown 1985; Schieb et al. 1999)). Symmetry has been shown to positively correlate with mating success in many animal species, while symmetrical human faces have been shown to be more attractive in experimental conditions (Grammer & Thornhill 1994; Perrett 1999; Schieb et al. 1999)).

1.3.3 Facial femininity/masculinity.

Investigations in to the effects of sexual dimorphism on facial attractiveness have revealed that femininity is attractive in the faces of both sexes (Perrett 1998). The feminine look is characterised by a high level of neoteny in facial characteristics (e.g. large eyes, high forehead, gracile facial features) and, as such, is to a large extent associated with looking young (Perrett 1998). The attractiveness of this facial type to men viewing women is explained by the associations between youth and fecundity: a young, but sexually mature, woman is capable of producing a larger number of offspring in the remainder of her reproductive life than an older woman. Women viewing male faces do not face a fecundity cut off in their mates, and instead appear to be avoiding negative personality attributions associated with increased masculinity such as dominance, infidelity and aggression (Perrett et al., 1998), which are undesirable characteristics in a man who may be raising children. These negative traits are, however, overwhelmed when women are at their most fertile (mid way through the menstrual cycle) at which point, it has been suggested, potential genetic benefits of a strong immune system, or attractiveness to fertile women, balance negative personality

traits associated with masculinity. Accordingly, when ovulating, female preferences for the faces of men shift towards those with more masculine characteristics (Feinberg 2006; Penton-Voak et al. 1999).

1.4 r/K selection and Life History Theory

The cascade of hormonal changes that take place during puberty irreversibly alter the appearance, endocrinology and behaviour of an individual human. The array of phenotypic changes that take place (the emergence of full secondary sexual characteristics, the commencement of sexual activity and behaviour) are all geared towards beginning reproductive life and the production of offspring. As has been noted, reproductive success is at the core of the evolutionary process. Consequently, events which surround reproduction are readily selectable. *r/K* selection theory and life history theory both provide an evolutionary framework for the investigation of the timing of human puberty.

Given that individuals are in competition with each other for the dissemination of their genes in the next generation (Dawkins 1979), one might expect most organisms to reproduce rapidly and produce many offspring in order to compete by weight of numbers of individuals sharing their genes in the next generation. Natural selection, however, tends to promote behaviours which are optimal to a given environment (Darwin 1859; Ridley 2004), and selective pressures may not favour the production of large numbers of offspring. This is because the production of any number of offspring takes time and energy which cannot be invested in any other activity (Borgerhoff Mulder 2000). Similarly, time and energy invested in one offspring can never be invested in another (Chisholm 1993). It follows, therefore, that the amount of investment possible in each offspring decreases with offspring number. There is, consequently, a trade off between offspring number and offspring fitness (or offspring quantity and offspring quality). The 'decision' by an individual

organism to adopt one side of the trade off over the other is informed by local environmental conditions (Borgerhoff Mulder 2000; Chisholm 1993; Stearns 1992).

r/K selection theory was formalised by MacArthur (1962; MacArthur & Wilson 1967). Drawn from evolutionary ecology, it is a framework accounting for the behavioural adaptations of a species to its environment in terms of reproductive strategy and energetic investment. According to the theory, organisms are driven by selective pressure down one of two broad directions respectively termed *r*- and *K*-selection where *r* is the growth rate of a population and *K* is the carrying capacity of the environment (the maximum number of individuals a given environment can sustain).

Organisms on the *r*-selected path are characterised by speedy maturation, rapid and prolific reproduction, the emphasis of offspring number over offspring fitness and low longevity.

Environments which promote *r*-selection have two possible formats. First, they can be extremely rich in resources and capable of supporting many more individuals than are present, meaning that parents can provide offspring with high levels of nutritional input for short periods of time before reproducing again (MacArthur & Wilson 1967). In primates, for example, high levels of environmental resources are associated with rapid reproduction and low inter-birth intervals (Dunbar 1988). Second, *r*-selection is associated with unstable, risky environments which have associated mortality risks from disease or predators. Under these circumstances, long term investment in offspring is not possible due to mortality risk while low numbers of offspring may be wiped out by environmental threats. This form of *r*-selection is common in many species of insects, bacteria, rodents and fish. *K*-selection is the result of more stable environments, where populations of organisms maintain a size near the carrying capacity of the environment due to the lack of mortality risk. *K*-selection emphasises offspring fitness over offspring number and promotes traits which lend advantage to individuals in competition for the environments' limited resources (MacArthur & Wilson 1967). Typical *K*-selected traits include large body size, increased longevity and the production of a small number of high-investment offspring. Silk, (1990) showed that

resource scarcity is associated with lengthy inter birth intervals in primates. Other K-selected organisms include many species of large mammal, such as elephants and the hominoid apes. The choice between r- and K-selection is not necessarily binary and there is a possibility that there is a continuum between the two extremes representing the extent to which a species allocates resources to offspring fitness over offspring number, or vice versa.

r- and K-selection accounts for the broad reproductive strategies of species as traits which are adapted to the local environment. *Homo sapiens*, for example, is a species on the extreme end of the K-selection path; sexual maturity takes place extremely late in life, inter-birth interval is long (up to 4 years in some hunter-gatherer populations) and offspring numbers are low (typically between 1 and 3 offspring per human couple). Life history theory, which has a similar basis to r/K selection theory not only accounts for inter-species variation in the allocation of resources, but provides a basis to examine intra-species differences in individual life course strategies in terms of allocation of energy and time.

Life history theory is an analytical framework which postulates that the suite of behavioural and physiological traits possessed by any individual organism may best be understood in terms of a series of key events and traits effecting and defining the life course of that organism (Borgerhoff Mulder 2000; Chisholm 1993; Stearns 1992). Examples of these traits are length of gestation, age at weaning, age of sexual maturity, age of cessation of growth and adult body size, age of first reproduction, number of offspring produced and interbirth interval¹. All of these landmarks involve activities which cost energy at the cellular level, either in terms of growth or repair of tissue (cellular meitosis, somatic effort) or of gamete formation (cellular meiosis) and reproductive effort. Given that an individual's energy, time and other resource budgets are finite, allocation of resources

¹ It should be noted that these exemplary traits are drawn from the life history of placental mammals. Life history theory is applicable to all living organisms, using landmark events and traits appropriate to the organism in question.

to life history events are likely to be influenced by selective pressures promoting optimal decisions (Stearns 1992), “an individual’s energy and resource budget is finite... tradeoffs are inevitable” (Borgerhoff Mulder 2000). Tradeoffs between growth versus reproduction, current versus future offspring and offspring quality versus offspring quantity are all predicted from life history theory (Stearns 1992). Each tradeoff is made according to the nature of the specific environment in which an individual finds itself.

Unstable environments, promoting r-selected species, put pressure on individuals to reproduce early and to reproduce often in order to maximise the chances of survival of at least some offspring and to increase phenotypic variation in offspring so that some may be better adapted to the shifting pressures of the local environment (MacArthur & Wilson 1967; Stearns 1992). This leads to an increase in inclusive fitness for the individual organism, despite the consequent low fitness of each offspring individually. Tradeoffs should reflect this strategy, with personal growth ceasing early in life in order to divert resources towards reproduction, early sexual maturity and first reproduction, low inter-birth intervals and large numbers of offspring. Stable environments, which have a low mortality risk but in which competition for resources is high (MacArthur & Wilson 1967), promote K-selected species and individual life history trajectories showing longer period of personal growth (leading to larger adult body size), later sexual maturity, long inter-birth intervals and smaller numbers of offspring, which are each individually fit, increasing their parents’ inclusive fitness accordingly.

There are two broad life history alternatives available to individual organisms, which are summarised (in extremely general terms) in figure 1. An individual can either emphasise the allocation of resources to reproduction at the expense of personal growth, and produce as many offspring as possible as early as possible (‘reproduce early, reproduce often’) or emphasise growth over reproduction, reaching a greater adult body size and reproducing at a slower rate with a higher inter-birth interval (‘reproduce later, reproduce slowly’). Since life history events include the

attainment of adult size and sexual maturity, the allocation of effort to one broad trajectory or the other has to be decided on early in life (Stearns 1992). Life history decisions should be based on early life experiences of an individual, which may, again using terms appropriate to placental mammals, include events that occur in the uterine environment, as long as those events can inform on the nature of the natal environment (Cowley et al. 1989).

The timing and/or magnitude of all life history events should align along the same trajectory, so that the effects of development in a given environment should be visible in every landmark. Life history events in primates have been shown to intercorrelate (Harvey & Clutton-Brock 1985). The age of sexual maturity has particular significance as a life history marker since it marks the period of cessation of growth and the attainment of adult body size as well as the development of secondary sexual characteristics and the attainment of reproductive maturity.

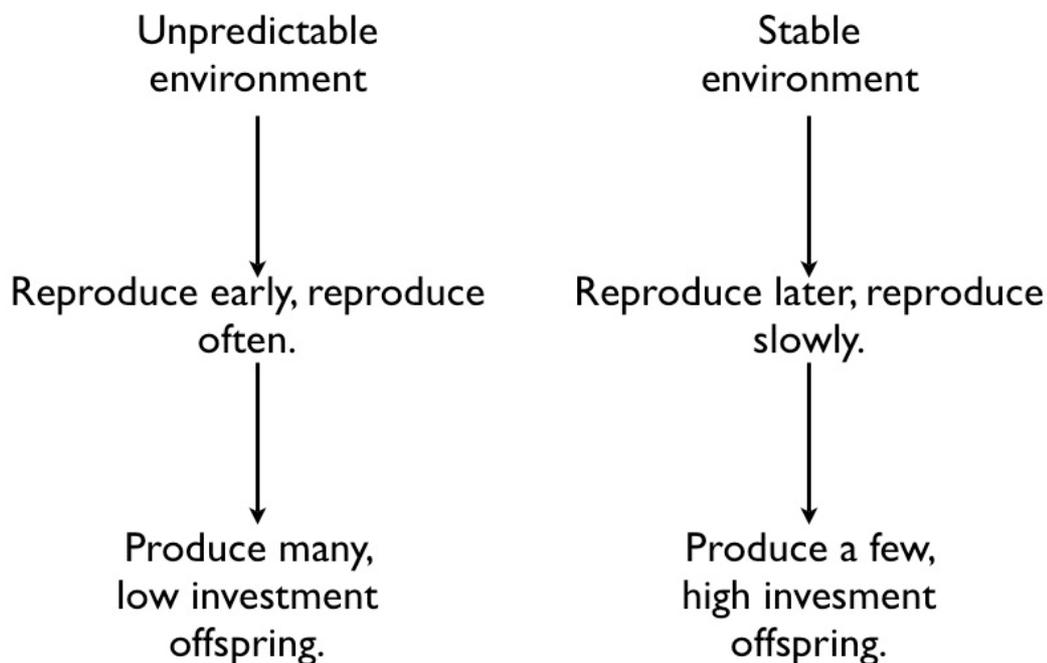


Figure 1-1: *Broad alternatives in life history trajectory*

1.4.1 Primate life history.

Between species variation in life history should be expected within an order of organisms. Since the work presented within this thesis focuses exclusively on humans, some discussion of the life history of the order to which humans belong is appropriate. The order *primates* contains approximately 250 species of animal ranging in size from 50g (the mouse lemur, *Microcebus* sp) to 200kg (the gorilla, *Gorilla gorilla*) (Fleagle 1999). Longevity ranges from 6 to over 50 years (Abrams & Rowe 1996), with humans displaying the longest lifespan of any primate (Sacher 1978). Similarly, primate social organisation shows great variation, ranging from solitary animals (e.g. the aye-aye, *Daubentonia madagascariensis*) to complex fission-fusion groups of sizes of over 250 individuals (e.g. the mandrill, *Mandrillus sphinx* (Setchell, 2006 pers comm)) and consequently face vastly different levels of intra-group resource competition. Given the vast range of body size, longevity and social organisation, primates are ideal animals on which to test and explore life history predictions. (Harvey & Clutton-Brock 1985) shows that primate life history variables (gestation length, neonatal weight, litter size, age at weaning, age at sexual maturity, age at first reproduction and longevity) all tend to align along the same trajectory and that primate life history, at the genus level, is intimately linked with adult body size which is, in turn, associated with differences in socioecology. (Smith 1989) added tooth eruption to the suite of life history landmarks available for study in primates.

Prosimian primates, the lemurs, lorises, galagoes and tarsiers, are, in general, smaller bodied, nocturnal insectivores (Fleagle 1999). They live in small groups, often solitary and are, as such, r-selected species with correspondingly rapid life histories (Kappeler 1996). Prosimians have a relatively low interbirth interval compared to the rest of the primate order and large litter sizes are common (Kappeler 1996); in many cases twin births are standard (Fleagle 1999). It is interesting to note that a diurnal prosimian, the ring-tailed lemur (*Lemur catta*), lives in large, social groups (as

most diurnal mammals tend to) and occupies a more K-selected niche, with a slow life history; they are larger bodied and longer living than most nocturnal, solitary prosimians (Kappeler 1996)

Anthropoid primates, the monkeys and apes, are larger bodied and typically more gregarious than prosimians. Living in larger groups, they face much heavier intra-group competition for resources and are, generally, K-selected species. Speed of development is slower in anthropoid primates than among the prosimians and longevity much longer. Life spans are particularly lengthy among the hominoids (the great apes (Wich et al. 2004)). The great apes also contain the largest extant primate genera; the gorillas (*Gorilla gorilla*) the adult males of which can reach 250 kg in body weight (Fleagle 1999). As the longest lived and largest primates, the hominoids also occupy the far ends of K-selection and have the slowest life history trajectories of all the primates (Wich et al. 2004). Sexual maturity occurs comparatively late, and the full expression of secondary sexual characteristics can be delayed until well in to adult life (Utami et al. 2002). Inter birth intervals are the longest of any primate genera, and offspring numbers accordingly low, with multiple births being extremely rare.

1.4.2 Sexual selection and Life History: speed of development as an adaptive trait.

Sexual dimorphism has been shown to correlate with the degree of polygyny in the mating system of a given species (Arnold 1984; Clinton & Leboeuf 1993). In pair-bonded, 'monogamous' mating systems, for example that of gibbons (*Hylobates*), there is little competition for mates and little intrasexual pressure. Consequently both sexes are morphologically similar to a high degree. Among polygynous animals (for example orangutans (genus *Pongo*), gorillas (*Gorilla gorilla*) and mandrills (*Mandrillus sphinx*)) intra-sexual competition for mates is high, typically among males (owing to the greater reproductive variance in males than in females, see section on mating strategy). There is correspondingly increased sexual selection on male animals towards the evolution of weapons and large body size which female animals do not face. Consequently, male

animals tend to be larger bodied and in possession of larger weapons (e.g. canine teeth in primates (Plavcan 2005; Plavcan & van Schaik 1992; Plavcan et al. 1995) antlers in deer (Kodric-Brown & Brown 1984)) than females. This leads to higher levels of sexual dimorphism in polygynous animals.

Darwin (1859) suggested that sex-limited traits should carry a survival cost because otherwise females would share them. The fact that males have lower longevity than females in most polygynous species supports this hypothesis (Clinton & Leboeuf 1993; Dittus 1977; Dittus 1979; Froehlich et al. 1981; Sherman 1984). Full sexual maturity is the point at which secondary sexual characteristics emerge, although males of many vertebrate species are capable of producing sperm before the emergence of secondary sexual characteristics (Zinner et al. 2005). If full sexual maturity and reproductive behaviour is associated with a cost to longevity, then delaying pubertal development may be a tactic to avoid the risks of early mortality associated with the development of secondary sexual characteristics (Clinton & Leboeuf 1993; Trivers 1972). It is, of course, likely that the risk of early mortality associated with early development is offset by the increased reproductive success the sexually dimorphic male traits offer, in terms of attracting females and competing against other males (Trivers 1972). Life history theory interacts with this phenomenon to predict that early development and increased mortality cost are offset by greater early reproductive success when longevity is low, either due to environmental pressure, increased social competition for resources (leading to mortality risk from resource scarcity or aggressive threats) or other health risks. As a consequence, the early emergence of secondary sexual characteristics should be associated with a 'reproduce early, reproduce often' type life history trajectory.

Male orangutans (genus *Pongo*) show variation in the expression of secondary sexual characteristics. Only males who control a territory develop the characteristic cheek flanges and throat sacks of a fully mature male orangutan (Utami et al. 2002). Other, subdominant males remain in a state of delayed maturation until such time as a local dominant male dies or is removed. The

unflanged males, despite not displaying full secondary sexual characteristics, are nonetheless reproductively active and are responsible for some 10% of the offspring produced in a dominant male's territory, while the flanged, dominant males enjoy much greater reproductive success (Utami et al. 2002). Life history theory would predict that the males who become flanged later would live for longer after the development of cheek flanges and large body size than males who become flanged earlier. At time of writing, no data has been reported on this hypothesis, presumably due to the problems with tracking individual orangutans and assessing age in the wild.

Humans show a modest degree of sexual dimorphism, in accordance with general adaptations towards low level polygyny as indicated by testicular volume (Harcourt et al. 1981), for example. Adult men are in general taller and heavier than adult women and are more robust in skeletal structure and facial appearance. The action of sex hormones at puberty, triggering the emergence of secondary sexual characteristics, overhaul physique and appearance to a much greater extent in men than in women who tend to retain juvenile characteristics (with the obvious exceptions of breast growth and changes in waist-hip proportions). Since human sexual dimorphism is consistent with an evolutionary history of modest male-male competition, we can infer costs associated with the emergence of secondary sexual characteristics in men, which is supported by the lower longevity of men compared to women and a peak in death rates in recently post-pubertal men that is characteristic of costs associated with development (Clinton & Leboeuf 1993). As with other animals showing sex-linked risks in sexual development, variations in human male life history should be associated with variation in reproductive strategy.

1.5 The process of puberty in humans.

The period of human pre-maturity is unusually protracted for an animal of our size. Even accounting for the unusual secondary altriciality in humans, human childhood represents a lengthy

period of time when young humans are dependent on others (mostly parents) for their care. Full emergence of secondary sexual characteristics is delayed by a lengthy period of adolescence. It is possible that human adulthood is delayed in order to extend the length of time for young humans to become fluent in the nuances of human behaviour and interactions within society (Bogin 1997).

At around 13 years old in boys and 12 years in girls (Argente 1999; Parent et al. 2003), human puberty tends to begin. Physically, the changes of puberty are marked first by a marked period of accelerated growth, in which normal rate of growth is markedly accelerated in most individuals, and especially in boys (Rogol 2002; Rogol et al. 2002). This take-off point is followed by a suite of physical changes including the growth of body hair, and facial hair in boys, maturation of the eccrine glands and the gradual development of an adult body shape and 'strengthening' of facial features. This last feature is particularly evident in young men, whose faces undergo a period of intense change; their brows becoming more pronounced and their jaws becoming more robust. In girls, puberty is also marked by breast growth and by the onset of menstrual bleeding (menarche). In boys, the voice 'breaks' and deepens and the testes begin producing sperm (spermarche). As the pubertal process nears completion, the growth rate slows and gradually stops in both sexes, generally leaving adult men taller than adult women (Argente 1999; Brook 1999; Parent et al. 2003; Romeo et al. 2002). Most of the physical changes of puberty can be put down to the action of the sex hormones testosterone and oestrogen and their metabolites.

In adults, sex hormones are secreted mainly by the gonads, mediated by the secretion of gonadotropin releasing hormone (GnRH) by the hypothalamic-pituitary axis (HPA). In both sexes, GnRH stimulates the production of testosterone and oestrogen by the gonads. Testosterone is regulated by negative feedback with the production of GnRH by the HPA (Veldhuis et al. 1992). In infants and children, the link between the HPA and the gonads is blocked by an unknown mechanism, although is active in human neonates immediately after birth (Brook 1999; Romeo et al. 2002). At the onset of puberty, the link is reestablished and the HPA produces a massive surge of

GnRH that is, in itself, diagnostic of the inception of puberty (Brook 1999). In response to the GnRH surge, the pituitary begins producing large amounts of luteinising and follicle stimulating hormones which, in turn, promote the release of sex hormones testosterone and oestrogen to different extents in both sexes (Brook, 1999; Romeo et al., 2002). Testosterone promotes bone growth, so the pubertal growth spurt is initiated. In both sexes the bones begin to thicken and become robust. Oestrogen inhibits bone growth and acts to slow the growth spurt. Testosterone is also responsible for the growth of body hair in both sexes and masculinisation of the larynx in men.

While the processes of puberty are comparatively well understood, the mechanism which begins the chain of endocrinological events is unknown, as is the nature of the break that occurs between the HPA and the gonads after birth. "The simple fact is, we have no idea how puberty is initiated" (Brook, 1991, p4). Puberty can be initiated at any age between a normal range of 9 years to 14 in boys and 8 years to 13 in girls (Parent et al., 2003; Argente, 1999). Exactly what factors contribute to the timing of puberty are unclear. There is a tendency of girls to develop at the same age as their mother did and timing of puberty is more similar in monozygotic (i.e. identical) than dizygotic twins which suggests that pubertal timing is at least in part genetically determined (Palmert & Hirschhorn 2003). However, there is a well reported tendency for socioeconomic status to influence age of puberty, particularly in girls, with early menarche being associated with poorer socioeconomic conditions (Mace 2000), and for early life experiences to effect age of menarche (Moffitt 1993; Moffitt et al. 1992). Given that reproduction is not possible until sexual maturity is reached, this is in line with life history predictions that early life stress, here socioeconomic stress, would lead to precocious development (Stearns 1992). Furthermore, there is substantial evidence that body mass is crucial in female puberty and that menarche is dependent on a certain critical body mass being reached. Not only do female victims of famine or anorexic girls show delayed puberty, but girls with higher levels of teenage adiposity display earlier menarche (Sloboda et al. 2007), although Koprowski et al, (1999) have linked this to energy intake rather than body mass *per*

se. Intriguingly, the hormone leptin, most well known for its central role in the physiology of weight gain (Friedman & Halaas 1998) has been shown to be crucial for the reactivation of the HPA-gonad link in rats (Cheung et al. 1997), mice (Ahima et al. 1997) and possibly humans (Keiss et al. 1999) although appears to be a facilitating factor rather than the mechanism for this reactivation in itself (Brook 1999).

1.5.1 Puberty and human life history

Work on primates has shown that age of sexual maturity should provide an index of life history trajectory. Similarly, in males, the age of emergence of secondary sexual characteristics should indicate life history speed. These effects should also be apparent in humans.

There is no data explicitly linking longevity to age of puberty in humans. However, Daly & Wilson (1997) have shown that humans living in environments with a high risk of early mortality (due to homicidal aggression) tend to begin reproduction earlier, suggesting a broad link between mortality risk from interpersonal aggression (a K-selection pressure) and an accelerated life history trajectory. Furthermore, associations between early puberty and low socioeconomic status has been reported in a variety of human societies (Mace, 2000). Since low socioeconomic status is a source of stress, this may represent an acceleration of life history in response to environmental stress that is in line with life history predictions. It has also been shown that girls placed under early life stress in terms of paternal absence or neglectful or abusive parenting tend to have an earlier menarche (Belsky 1997; Moffitt 1993), which is also in line with life history predictions that early life stress will inform an individuals allocation of energy to either reproduction or growth. Age of puberty in humans appears to interact with behavioural and environmental differences in ways entirely consistent with a life historical approach.

1.6 A note on retrospective reporting of puberty.

This thesis relies on retrospective recall of puberty in adults. There are immediate problems with reliability when asking participants to recall the age at which they became sexually mature, not least of which is the potential for participants to misremember or fabricate evidence for an event which cannot be directly observed. This problem is addressed by Ostovich & Sabini (2004). As they do, this thesis will proceed to analyse and discuss data as if reported age of puberty reflects accurate memory. There is a further problem with assessing pubertal timing in men. Age of menarche has been shown to be a reliable indicator of human female pubertal timing which remains a resilient and memorable landmark across the lifetime of a woman (Kaiser & Gruzlier 1999) and has been used in many studies as a retrospective marker of physical maturity. By contrast, no equivalent single event stands out in male physical development that can be used as a retrospective indicator of puberty, while indices involving age of first shave, first nocturnal emission or deepening of the voice show varied success as puberty indices. Kaiser and Gruzlier (1999), while presenting a scale for the retrospective recall of puberty, report that, while age at menarche proves an accurately recallable indicator of puberty in women, men “seem to be able to judge their pubertal timing in relation to others, but seem less sure about the timing of specific events” (p66). As they recommend, two items are used in this thesis to assess pubertal timing in the adult subjects: age of first shave (or menarche for those experiments involving female subjects), and timing of puberty with reference to peers at the time (*Compared to your peers at the time, did you go through puberty... response on a Likert-type scale from 1 (much slower) to 7 (much faster)*). Based on the work of Kaiser and Gruzlier (1999), it is expected that the relative puberty speed question will provide more accurate information for the male subjects.

1.7 Dominance

1.7.1 Dominance hierarchies in the animal kingdom

The formation, maintenance and behavioural and biological implications of dominance hierarchies among various animal species have been the focus of ethological studies for many years. Primates, in particular the anthropoid primates, have particularly well studied dominance systems. Definitions of dominance, from an ethological perspective, tend to centre around the observation of dominance, that is, defining the dominance of an individual animal in terms of its observed behaviour. For example, Rowell (1963) and Seyfarth (1976) both define primate dominance in terms of approach and retreat behaviours while Koyama (1967) and Hausfater (1975), using similar cues, define dominance in terms of directionality of agonistic and aggressive acts. These definitions help to identify dominant and subdominant individuals in any interaction, but do not define the concept of dominance. Dominance interactions occur between individuals, often in dyads. Repeated dyadic interactions within a group cause a dominance hierarchy to emerge (Pellegrini 2002); individuals are not intentionally acting to cause a hierarchy, but their repeated interactions nevertheless form and maintain a fluid dominance system. Dominance, as with any behavioural trait, must be considered in terms of the benefits it provides to individuals, rather than as an end in its own right (Pellegrini 2002) an immediate benefit of high dominance is access to resources, whether that be in terms of food, territory or, crucially to this thesis, mates (Hawley 1999; Pellegrini 2002)

1.7.2 Dominance and Mating Strategies

Dominant male primates often appear to have greater reproductive success, in terms of priority of access to females (Small 1993). Oestrous female capuchin monkeys (*Cebus apella*), for example, will often approach and display to the dominant males of the troop and allow them to mount before any subdominants are permitted to approach (Janson 1984). The territory-controlling, dominant

male orangutan (*Pongo pygmaeus*) has, within his territory, smaller territories belonging to several females, to all of whom he has sexual access which he will defend against other males. Given that dominant males seem repeatedly to have priority of access to receptive females, it seems surprising that dominants do not father all the offspring in their communities yet genetic paternity tests show that dominant males, in fact, father about half of the offspring on their territory (Utami et al. 2002) and are by no means the only successful breeders. If dominant males are not fathering all the offspring, then subdominant males, logically, must have found a way to compete.

The male three-spined stickleback (*Gasterotus aculeatus*) comes in two distinct morphs. One is large, brightly coloured and behaves in a way that is likely to draw the attention of predators; the other is small and drab and keeps itself well hidden. The only other difference between the two males is that the former controls a territory, while the latter does not. The territorial male (hence resource-controlling, hence dominant) is approached by an egg-bearing female who may release her eggs into the water column for the male to fertilise. All else being equal, the territorial male will outcompete the non-territorial male since females will only mate with males that control a territory. The nonterritorial male, however, has evolved a 'sneaking' strategy that involves lurking on the perimeter of another male's territory, waiting for a female to release her eggs in response to the territorial male and moving in (at high speed) to release sperm onto the eggs (Lagardier et al. 2001; le Comber et al. 2003; Whoriskey & Fitzgerald 1994).

Such alternative, 'sneaking' strategies are not unique to teleost fish. The discovery that the subdominant, unflanged, smaller male orangutans that are frequently observed on the territories of dominant males are neither juvenile males nor sons of the dominant male has led to the identification of a subdominant mating strategy among the pongids (Utami et al. 2002). The larger bodied, flanged, dominant male orangutans travel to the territory of one of the females on his territory and calls for her until she comes to him, which she will since there are great benefits of mating with a dominant male in terms of resources for and protection (against other males) of

herself and her offspring. The smaller, unflanged, subdominant males travel around the females' territories, looking for a receptive female with whom they will attempt mating, often by force. It seems, in fact, that subdominant males can harass receptive females to such an extent that protection from the subdominants is the greatest benefit (and consequently the largest influence on mate choice) that consortship with a dominant male orangutan can offer (Fox 2002). The two strategies available to male orangutans can be broadly termed 'sitting, calling and waiting' versus 'going, searching and finding' (Maggioncalda et al. 2002; Utami et al. 2002). The subdominant males of both the sticklebacks and the orangutans need to be highly attentive to cues of sexual receptiveness and female presence if they are to successfully operate their strategies. The non-territorial stickleback male must, for example, be able to time his dash into and out of the other male's territory to perfection; too early and he will be spotted and chased off, too late and the dominant male will release his sperm and fertilise the eggs (Le Comber et al., 2003). The non-territorial male must respond to the release of eggs faster than the territorial male does. Similarly, an unflanged male orangutan would be well served by being much more sensitive to the presence of an oestrus female than a dominant male since not only does he have to find her first (because she will preferentially mate with the dominant as soon as he arrives) but the female will move towards the dominant as soon as he calls; the dominant male does not need to be as finely aware of female presence as he does not have to find her (Utami et al. 2002). This should promote mate guarding behaviour in dominant males and vigilance against strategies of subdominants. Furthermore, dominant males may be expected to be acutely aware of female reproductive condition in order to appropriately guard their mates (for example, a male should be expected to preferentially guard an oestrus female since copulations with other males would be more likely to lead to conception). For these reasons, male dominance should be expected to impact not only on mating strategy but on attendance to cues of reproductive condition in females. This possibility is addressed in Chapter 5.

1.7.3 Dominance hierarchies in humans

Phylogenetic analysis has suggested that dominance hierarchies are a primitive condition for primates and are particularly well established among the hominoids (Ghiglieri 1987). Since humans are hominoid primates, we have every reason to predict that dominance associated behaviours will be visible in humans. Analysis of speaking time in groups of same-sex strangers suggests that humans form dominance hierarchies very quickly (within 5 minutes of first meeting in men) that then persist over time (Mast, 2001). Repeated work shows that human females value resource control in potential mates, while analysis of lonely hearts columns shows that males are more likely than females to advertise their status in terms of resource control (Koziel & Pawlowski 2003; Pawlowski & Dunbar 1999), control of resources being inextricably linked with dominance (Hawley 1999). Investigation into rank on a military base in the US shows that access to females (in terms of having a second family) as well as reproductive success (in terms of offspring produced) positively correlate with rank attainment (Mueller & Mazur 1998). In general, human females seem to find resource controlling (hence dominant) males highly attractive. The effect can be seen cross-culturally also, for example among the Yanomamo of the Amazon basin. Social status among male Yanomami is overtly linked to aggression and physical prowess. A male achieves special status when he has killed (normally a male from a neighbouring, rival village), and is recognised as being a man. High numbers of kills and reputation for skill in battle increase the status of Yanomamo males, in terms of their *waiteri* (loosely translated as “ferocity” or “courage”). Males with higher *waiteri* are not only well respected and highly influential in their village, but also have greater access to wives and, often, more children than low *waiteri* males; intimately linking social status with reproductive success (Borofsky 2005; Chagnon 1967).

Studies of human mating strategy has often revealed the existence of a large variation in within-sex strategy (Gangestad & Simpson 2000), although the variation within males has often been

considered in terms of low-high investment strategies, in line with a dual-mating strategy operated by females that drives them to preferentially select high masculinity males at the high-fertility phase of the menstrual cycle due to the genetic benefits they offer their offspring (in terms of immunocompetence since testosterone is an immunosuppressant (Folstad & Karter 1992; Olsson et al. 2000) and low masculinity (high femininity) males the majority of the time due to the care and attention they offer for females and their offspring (Gangestad & Simpson 2000; Penton-Voak et al. 1999; Penton-Voak & Perrett 2000). The possibility that dominance could also drive variation in mating strategy can now also be explored.

1.8 Mating Strategies

1.8.1 The evolution of mating strategies; between-sex differences.

Sexual selection, as defined by Darwin (1871) has two components; the competition between members of one sex for access to opposite sex mates, termed *intrasexual competition*, and the selection of a mating partner from a number of opposite sex competitors, *intersexual competition* (or epigamic competition). The former tends to promote the evolution of large body size and weaponry in the sex in which competition is higher (typically males in the animal kingdom), the latter is associated with the evolution of ornaments or behavioural displays (Andersson 1991; Plavcan & van Schaik 1992))

The process of sexual selection has led to a broad difference in mating strategy between males and females throughout most of the animal kingdom. Each sex has different costs and benefits associated with mating decisions, most of which are the result of fundamental asymmetries in the respective costs of male and female reproduction (Oliver & Hyde 1993).

The first asymmetry stems from differences in obligatory investment in offspring. Ova are more energetically expensive to produce than sperm (anisogamy, (Parker 1972)) meaning that costs of reproduction are higher for females even pre-conception. Following successful fertilisation of an ovum, the female animal typically gestates the developing foetus, which again takes up time and large amounts of energy. For mammalian females, there is a further, post-natal cost of lactation. These features are inescapable for most females and represent enormous costs to time and energy budgets, both of which are finite (Barber 1998; Kaplan 1996; Trivers 1972). By contrast, the only obligatory investments faced by mammalian males are the negligible costs of energy spent finding and attracting a mate, copulating and ejaculating. This asymmetry was first formalised by Trivers (1972) as Parental Investment Theory.

The second asymmetry originates in the different variance in reproductive success between the sexes. The time taken up by gestating offspring means that females face an upper limit on the number of offspring that can be produced in their lifetimes. This means that the numbers of offspring produced by individual females will tend to cluster around the mean for all females of that species; a female who does well will not do much better than a female who does poorly, in terms of number of offspring produced. Male reproduction, by contrast, is limited only by access to females. A highly successful male can impregnate a high number of females and produce many more offspring than a less successful male. Consequently, reproductive variance is higher for males than for females (Bateman 1948; Haselton 2003; Symons 1979).

These asymmetries have a number of effects on the optimal mating strategies for men and women. An optimal strategy for a man would consist of multiple matings with multiple partners in order to maximise the occurrence of his genes in the next generation through weight of numbers (Krebs & Davies 1993; Oliver & Hyde 1993; Symons & Ellis 1989). By contrast, given that the number of children a woman can produce across her lifetime is limited by her physiology, a woman's optimal mating strategy would be to reproduce with a partner likely to offer her and her potential offspring

sufficient resources and protection to ensure her children survive to reproductive age and her genes pass in to the next generation. If men are attempting to implement a strategy where conception and child production is of paramount importance, then their mating strategy should reflect a preference for cues related to fertility and fecundity in potential female partners and for a high number of short-term, sexual relationships (Gangestad & Simpson 2000). Similarly, female mating strategy should be characterised by attention to cues relating to resource accrual, fidelity and parental investment (Thornhill & Gangestad 1999) and a preference for long term, committed relationships.

1.8.2 Within-sex variation in mating strategy: “Which men, which women?”

The identification of optimal strategies for men and women does not offer grounds to assume that all individuals of a sex will adopt the same reproductive tactics. The point is clearly explained by Gangestad and Simpson (2000, p577):

Consider a parallel example where the currency of profit is money rather than fitness. Suppose that brain surgeons make more money than anyone else does. Clearly it is not the “most profitable” money-making scheme for everyone to decide to become a brain surgeon. Only so many people can become brain surgeons; hence, most people would be bound to fail. Instead, the most profitable strategy for most people would be to select careers that provide them with the most money, given their abilities, and, in competitive markets, their chances of success.

In other words; operating the optimal mating strategy is only viable if an individual’s attributes make success likely. If a man *can* attract and impregnate multiple women, then that would become his optimal strategy (assuming for the sake of argument that all children are guaranteed to reach maturity without his investment). If we suppose that only males who are highly physically attractive can attract women for short term matings in this way, then the problem becomes clear; in a mating arena where males differ in their physical attractiveness, only a certain number of men will be able to attract multiple, serial partners. Other males should be expected to moderate their strategy to play to their own strengths and abilities within a competitive mating market and adopt different mating strategies. In fact, there is evidence to suggest that the within-sex difference in mating strategy that

this rationale implies is greater than that which exists between the sexes (Gowaty 1992; Simpson & Gangestad 2001; Simpson et al. 1999).

1.8.3 Dominance and puberty as sources of variation in mating strategy.

1.8.3.1 Puberty and mating strategy.

One of the central premises of this thesis is that earlier puberty is symptomatic of a developmental trajectory emphasising early and prolific reproduction. A mating strategy associated with a rapid life history should be characterised by a preference for short-term matings and, therefore, an unrestricted sociosexuality (see Chapter 2). The alternative, long-term mating strategy, typified by a preference for monogamous relationships and a more restricted sociosexuality, should be associated with a slower life history trajectory and later puberty. This difference in mating strategy should be evident in the type of female face early developing men find attractive (see Chapter 3) as well as in their preferred traits in an ideal partner (see Chapter 4).

1.8.3.2 Dominance and mating strategy

Among many animal species, dominance is associated with increased reproductive success and preferential access to mates (Ellis 1995; Janson 1984; Small 1993; Utami et al. 2002).

Consequently, dominance is often coincident with high mate value. Chapter 9 will investigate the link between male dominance and attractiveness.

High mate value individuals are by definition very attractive and, as such, can select mates who are also high in mate value. Consequently, high mate value individuals can afford to be more discriminating in their mate choice (Gangestad & Simpson 2000). Men attend to physical cues of health, youth, fertility and fecundity in women (Thornhill & Gangestad 1999). Femininity, as an indicator of youth and fertility, is inextricably linked to female attractiveness (Perrett 1998;

Thornhill & Gangestad 1999). Consequently, high mate value men will be more discriminating of these cues than low mate value men and will show increased preferences for femininity, since they are more likely to attract more attractive women (Gangestad 2000). By contrast, low dominance men should not expect to attract high mate value women and consequently be less discriminating of femininity or attractiveness in their partner.

Resource control and strength are useful traits to ensure offspring survival in either sex.

Consequently, dominant males should show a preference for females exhibiting cues of dominance.

In humans, this should be true to the extent that dominance does not equate with masculinity in females, since masculinity may have a detrimental effect on female attractiveness .

If dominant men are attractive men (see chapter 9), then they should be able to capitalise on their attractiveness by operating the prototypical male strategy of maximising reproductive success by attracting multiple mates (Gangestad 2000; Gangestad & Simpson 2000). This strategy should, all else being equal, be optimal for males. Consequently, dominant men should be more inclined to have multiple sexual partners and be more at ease with casual sex and, as such, should demonstrate a more unrestricted sexuality (high interest in casual sex) than subdominant men (Gangestad 2000; Gangestad & Simpson 2000; Simpson & Gangestad 1991). That said, the advantage to dominant males of preferential mating with females is lost if the females are inclined towards multiple matings since this would undermine their paternal certainty. Dominant men should, therefore, be less tolerant of high sociosexuality in women. By contrast, subdominant men should be more attracted to high sociosexuality women as they are less likely to discriminate against them.

2 Pubertal timing, dominance and mating strategy 1: Sociosexuality Orientation.

2.1 *Abstract*

Both pubertal timing and dominance have been proposed as sources of variation in within-sex mating strategy, through their links to life-history trajectory and mate value respectively.

Differences in (heterosexual) mating strategy should be apparent in sociosexuality (a measure of interest in casual sex). In this chapter, we test the hypothesis that unrestricted sociosexuality will associate with early puberty and high dominance. In a sample of 9,029 men, split in to two age groups (18-30 years and 31-65 years) we find that both early puberty and high dominance are associated with unrestricted sociosexuality in support of the hypothesis.

2.2 *Introduction and hypotheses*

This chapter reviews behavioural manifestations of sexual reproductive strategy in terms of restrictedness or openness to casual sex as measured on the Sociosexuality Orientation Inventory scale. Hypotheses are derived relating both dominance and puberty to this characteristic.

2.2.1 *Sociosexuality*

The difference in *optimal* relationship type for men and women (i.e. short-term vs. long-term relationships) should lead to differences in attitudes towards sex and commitment. Anecdotally, men do appear to be more interested in casual sex with multiple partners than women do, although this observation is of little use unless it can be quantified. One method that exists for the quantification of attitude towards casual sex is the Sociosexuality Orientation Inventory.

Sociosexuality is a measure of the degree of comfort with which an individual approaches casual sex (Gangestad & Simpson 1990; Gangestad & Simpson 1992; Gangestad & Simpson 1993). Individuals with a *restricted sociosexuality* tend to avoid casual sexual encounters and need to be strongly attached to a partner before sex. *Unrestricted sociosexuality* represents the converse attitude, where casual sex without emotional commitment is acceptable to an individual, if not necessarily preferred. People in the former category tend to have more sexual partners and have first sex at an earlier age than those in the latter (Gangestad & Simpson 1993). Gangestad and Simpson developed and validated a seven point construct to measure variation in sociosexuality; the Sociosexuality Orientation Inventory (SOI, (Gangestad, 1993). The SOI is comprised of two subscales, one gathering behavioural data on sex (number of partners in the last year, number of partners foreseen in the next 5 years, number of ‘one-night stands’ in total, and frequency of sexual fantasy from 1, *never* to 7, *more than once a day*) and one gathering attitudinal data (agreement/disagreement with three statements on a 9 point scale: *sex without love is ok, I could imagine myself being comfortable having sex with multiple partners* and *I would have to feel closely attached to someone before I could completely enjoy sex with him or her*). These variables are entered in to a formula provided by the designers of the scale². The resulting numerical scale forms a relative scale ranging from low-scoring, restricted individuals to high-scoring unrestricted individuals. Men score consistently higher on the SOI than women (Simpson & Gangestad 1991), reflecting a greater interest in casual sex among men. The SOI does not correlate with sex drive or sexual satisfaction, but has been shown to relate to mate preferences; Simpson & Gangestad (1991) showed that individuals with low, restricted SOI scores tend to rank wealth and other factors related to status and resource control as highly attractive, whereas individuals who show unrestricted sociosexual orientation, scoring high on the SOI, tend to value physical attractiveness more in a

² $5(\text{number of partners in the last 12 months})+(\text{number of partners foreseen})+5(\text{number of one night stands})+2(\text{frequency of sexual fantasy})+2(\text{a statistical amalgamation of attitudinal measures})$

partner. Unrestricted individuals are expected to begin having sex at an earlier age and to have more sexual partners and a higher frequency of intercourse than those with a restricted sociosexuality. As such, there are parallels between behaviours associated with sociosexuality orientation and attachment style as proposed and defined by (Bowlby 1971) and (Belsky 1997). Whereas attachment style is a purely psychosocial trait, reflecting the ease with which an individual forms and maintains close relationships, there is some evidence to suggest that sociosexual orientation is, at least in part, genetically determined (Gangestad & Simpson 1990) and may run in families (Bailey et al. 2000).

2.2.1.1 Puberty and Sociosexuality

If early puberty represents preferential allocation to early reproduction over growth according to life history theory, then it should be associated with behaviours that maximise the chances of reproductive success and offspring number. A preference for short-term relationships and casual sex would be one such behavioural correlate for men, since it increases the likelihood of conception with multiple women. Consequently, men developing early should be expected to display unrestricted sociosexuality (Ostovich & Sabini 2005).

2.2.1.2 Dominance and Sociosexuality

If dominant men are attractive men (see Chapter 9), then they should be able to capitalise on their attractiveness by operating the prototypical male strategy of maximising reproductive success by attracting multiple mates. This strategy should, all else being equal, be optimal for males (see Chapter 1). Consequently, dominant men should be more inclined to have multiple sexual partners and be more at ease with casual sex and, as such, should demonstrate a more unrestricted sociosexuality than subdominant men.

Based on all the above, the following hypothesis is advanced:

Unrestricted sociosexuality in men will be associated with early puberty and high dominance.

2.3 Method

An internet-based survey was launched during a 2005 collaboration with the BBC, who were producing a documentary series on human gender roles and sex-typical behaviour. Participants were directed to the site from the BBC science webpages, and were asked to complete a number of tasks related to various different aspects of human psychology and behaviour. Participants provided information basic demographic information, as well as information on their developmental history, dominance and anthropometric characteristics (e.g. weight and height). The complete internet survey included a mixture of tasks and questions to produce 222 variables many of which are not relevant to the current study. Ensuring the participants completed all questions in the survey was a prime concern. As such, during questionnaire design, there was often a trade off between the sophistication of questionnaire items and the length of the complete survey.

The use of the internet as a tool for gathering samples of this nature raises questions of participant reliability in uncontrolled conditions. Beyond the exclusion criteria (see below) which were employed to remove participants whose data were obviously untrustworthy, participants were assumed to be answering questions as honestly as laboratory based participants. Ross et al. (2005) have shown in an analysis of Swedish sexual health data, that online participants respond to surveys asking for personal information in indistinguishable ways from those completing surveys in more 'traditional' (e.g. lab-based) conditions.

Social and physical dominance were measured by asking participants to complete a statement (*Socially / Physically I am mostly...*) on a seven point scale from 1 (*submissive*) to 7 (*dominant*).

Participants were also asked to rate their own attractiveness on a seven point scale from 1 (*not at all attractive*) to 7 (*extremely attractive*) on four different attractiveness scales; general attractiveness,

voice attractiveness, body attractiveness and face attractiveness. Puberty was assessed using two questions; age of first shave (in years) and speed of puberty relative to peers (*Compared to my peers at the time, I went through puberty...*) from 1 (*very slowly*) to 5 (*very fast*). Participants completed the various SOI measures as outlined above. Participants also completed a range of demographic questions (current age, country of residence, ethnicity, sexual orientation etc) and provided information on their sexual orientation.

From the complete internet-sample of over 250,000 individuals world-wide, UK national, self-certified heterosexual caucasians aged 18-65 years (mean 33.25 years) were extracted. The resulting dataset was screened for duplicate IP addresses and abnormal responses to target questions (e.g. individuals who declared their age of first shave to be younger than 10 or older than 20 were excluded). Finally, participants who responded that they had not answered questions honestly while completing the questionnaire (n=10) were excluded. The complete sample contained 9,029 males.

Since the age range in the sample is large, there is potential for inter-generational differences in pubertal timing to influence results. Participants were split in to two age groups around the median age for the sample (30 years); 18-30 year-olds (n=4,594, mean age=23.70 years, SD=3.63) and 31-65 year olds (n=4,435, mean age = 41.99 years, SD=8.44)

SOI attitudinal items were Z-scored and averaged before SOI score was calculated as outlined above (see section 2.2.1).

Self rated attractiveness and self rated dominance scores were calculated for each group by separately factor analysing the four attractiveness questions and the social and physical dominance questions. All attractiveness variables loaded on a single factor for each group, accounting for 64.31% and 67.22% of the total variance for the younger and older groups respectively. Both social and physical dominance also load positively on the same factor, accounting for 71.78% of the variance in the youngest age group and 74.40% of the variance in the oldest group. Attractiveness

and dominance factors were also produced for the entire sample, which accounted for 65.73% and 73.04% of the variance respectively.

2.4 Results.

2.4.1 Sociosexuality

6,704 participants successfully completed all items on the Sociosexuality Orientation Inventory (SOI). Whole sample mean SOI = 24.04, SD=34.18. Kolmogorov-Smirnoff tests reveal that SOI score is non-normally distributed for the entire sample ($p < .0001$). Spearman's rank order correlation shows that SOI score correlates positively with overall self-rated attractiveness factor [$r = .21$, $n = 6,646$, $p < .0001$], which is in line with predictions that attractive men would be more likely to operate a short-term mating strategy (Gangestad & Simpson 2000). In the whole sample, SOI score correlates positively with relative puberty speed [$r = .04$, $n = 6,678$, $p = .002$] and negatively with age at first shave [$r = -.07$, $n = 6,576$, $p < .0001$]. This provides support for the hypothesis that earlier developing men would have a more unrestricted sociosexuality. Similarly, the dominance factor correlates positively with SOI score across the whole sample [$r = .15$, $n = 6,683$, $p < .0001$], supporting the broad hypothesis that high dominance men would be more prone to engage in casual sex than low dominance men.

2.4.2 Sociosexuality by Age Group

Kolmogorov-Smirnoff tests show that no variable in either age group is normally distributed ($p < .0001$).

Among the 18-30 year olds, Spearman's rank order correlations show that relative puberty speed correlates positively with SOI score [$r = .06$, $n = 3,408$, $p = .001$] while age at first shave correlates negatively with SOI score [$r = -.05$, $n = 3,351$, $p = .01$]. Dominance factor (as calculated for the younger age group) correlates positively with SOI score [$r = .20$, $n = 3,405$, $p < .0001$], as does attractiveness factor [$r = .24$, $n = 3,388$, $p < .0001$]. Age in this group does not correlate with puberty

speed [$r=-.02$, $n=4,382$, $p=.13$], but does correlate with age at first shave [$r=-.04$, $n=4,279$, $p=.01$], SOI score [$r=-.04$, $n=3,416$, $p=.02$] and self rated attractiveness factor [$r=.04$, $n=4,362$, $p=.01$]. All variables were rank transformed and entered in to a partial correlation, controlling for rank of age. The correlations between SOI score and self rated attractiveness, [$r=.24$, $n=3,308$, $p<.0001$], self rated dominance [$r=.19$, $n=3,308$, $p<.001$], puberty speed [$r=.05$, $n=3,308$, $p<.01$] and age of first shave [$r=-.04$, $n=3,308$, $p=.01$] are all maintained showing that these relationships are independent of their relationship with age.

Among the 31-65 year olds, spearman's rank order correlations reveal that relative puberty speed does not correlate with SOI score [$r<.01$, $n=3,225$, $p=.83$] but correlates negatively with age at first shave [$r=-.05$, $n=3,225$, $p<.01$]. Dominance factor correlates positively with SOI score [$r=.12$, $n=3,278$, $p<.0001$], as does self rated attractiveness factor [$r=.16$, $n=3,258$, $p<.0001$]. Within this age group, age correlates with age at first shave [$r=.14$, $n=4,122$, $p<.0001$] and negatively with attractiveness [$r=-.08$, $n=4,201$, $p<.001$] and SOI [$r=-.13$, $n=3,288$, $p<.0001$] but not with relative puberty speed [$r<.01$, $n=4,213$, $p=.80$]. Variables were rank transformed before partialling out age. The correlation between self rated attractiveness and SOI score is maintained [$r=.12$, $n=1,570$, $p<.0001$] as is the relationships between SOI and self rated dominance [$r=.11$, $n=3,175$, $p<.0001$]. The relationship between SOI and age of first shave has become a non-significant trend [$r=-.03$, $n=3,175$, $p=.08$].

Earlier puberty is associated with unrestricted sociosexuality in the 18-31 year old men and to some extent in the 32-65 year old men. This provides support for the hypothesis.

2.5 Discussion and Conclusion

Some of the significant correlations reported in this chapter are extremely small with r^2 , in some cases, at less than .05. The smallness of these effects is likely to reflect the fact that there are many other factors, unmeasured in this sample, which may influence, for example, self rated

attractiveness other than age and which may do so at a greater level than those relationships reported here. The size of this dataset has allowed some very small effects which may have not been visible in a smaller sample to be detected. It is further possible that a side effect of having a large sample is a shrinking of effect sizes, reflecting the increase in amount of statistical 'noise' which would increase as a proportion of sample size.

SOI score and puberty variables in the younger age group show the expected relationship in support of the hypothesis that early developing men will have a more unrestricted sociosexuality. This relationship may represent a behavioural aspect of life-history trajectory since men on a 'reproduce early, reproduce often' path would be expected to demonstrate a greater than average interest in casual sex in order to maximise numbers of sexual partners and, thereby, the chances of conception. By contrast, later developing men who are, in theory, operating a high investment reproductive strategy should be expected to be less interested in casual sex and more prone to long term relationships. The correlation between puberty variables and SOI score supports this conjecture. The relationship between dominance and SOI score is also in the predicted direction in that increased dominance is associated with unrestricted sociosexuality in both age groups. This provides support for the hypothesis, in that dominant men may be capitalising on their increased mate value by having multiple sexual partners and thereby increasing their chances of reproductive success in terms of offspring number.

3 Pubertal timing, dominance and mating strategy 2: preference for female faces.

3.1 Abstract

Early puberty and high dominance men should be acting to maximise their chances of conception with multiple female partners. This should have an impact on their preference for femininity (an indicator of fertility) and cues to sociosexuality in the female face. In this chapter, we hypothesise that early developing and dominant men will show increased preference for femininity. We further advance a hypothesis that puberty and dominance will impact on male preference for sociosexuality in the female face. In the same sample of 9,029 men from Chapter 2, we find that neither pubertal timing nor dominance have any relationship with femininity preference, although dominance, but not puberty, is associated with a preference for unrestricted female faces. Results are discussed with reference to a dominance-dependent male mating strategy.

3.2 Introduction

3.2.1 Facial Attractiveness and Mating Strategy

Behaviours that promote the presence of an individual's genes in the proceeding generation(s) will be favoured by natural and sexual selection. Given that reproduction is crucial to the presence of an individual's genes in the next generation, behaviours surrounding mate selection are prime targets for sexual selection to operate (for sexually reproducing species). Individuals who select healthy, fertile and fecund mates are much more likely to reproduce successfully and prolifically and, therefore, increase the proportion of their genes in the next generation. Individuals who attend to signals of mate quality, therefore, are much more likely to select successful mates, assuming that

such signals are honest more often than chance. Sexual selection favours individuals who can accurately determine the fertility, fecundity and health of potential mates and thereby increase their chances of successful mating. The central themes of human facial attractiveness have been reviewed in Chapter 1.

3.2.2 *Preferences for Femininity*

If a human male is operating a short-term mating strategy, where rapid reproduction is paramount, then it follows that he should be attentive to signs of female fertility, since rapid conception is the focus of his strategy. This is not to say that cues of fertility are unimportant to men operating a long-term mating strategy, since ability to conceive is obviously crucial to the success of any mating strategy. Short-term strategists, however, should be *more* attentive to cues of fertility than long-term strategists, to whom cues of fidelity (or at least cues suggesting that a mate may easily be guarded from other males) may be more important. Given that female fertility is associated with increased facial femininity (Law Smith et al. 2006), this should mean that early developing men show a stronger preference for femininity in female faces (as reported in Cornwell, (2006a)).

Symmetry and averageness are traits that should be important to all individuals, regardless of mating strategy, as they do not directly signal fertility but may signal health and immune system quality. That said, cues of physical attractiveness should be more important in general to short-term strategists than to long-term. This possibility will be addressed in Chapter 4.

Both early puberty and high dominance have been hypothesised as being associated with a short-term mating strategy (see Chapter 1), while Chapter 2 has offered some experimental confirmation of this proposition, using sociosexual orientation as a measure of mating strategy. Consequently we should expect both early developing and high dominance men to display preferences for female faces which are consistent with a short-term, multiple partner mating strategy.

3.2.3 Preference for Sociosexuality Orientation

Boothroyd et al. (2004; Boothroyd et al. 2007) have shown that individuals can accurately differentiate between composite faces made from individuals with low SOI scores (restricted) and those with high SOI scores (unrestricted), which suggests that cues to sociosexuality exist in the face. Furthermore, Burt et al. (2007) have shown that high and low SOI scoring men prefer different types of female face, showing that sociosexuality can directly impact on mate choice through face preference. Burt et al. also show that female faces selected by men for short-term relationships appear more feminine than those selected for long-term relationships.

Given that both early puberty and dominance have been shown to associate with unrestricted sociosexuality, there are grounds to predict that they will also associate with preference for cues of sociosexuality in the female face. Both early developing and dominant men should be expected to be attempting to maximise copulation number (and hence conception rate), it is, therefore, reasonable to predict that these men will be attracted to women who are most likely to be amenable to short term matings (i.e. those with an unrestricted sociosexuality). Dominant men should, therefore, prefer cues to unrestricted sociosexuality in female faces. That said, there is an alternative hypothesis that high dominance men will be more inclined to avoid unrestricted sociosexuality women in order to guarantee as far as possible their paternal certainty. Among other, non-human primates, dominant males often engage in particularly vigilant mate guarding (e.g. Watts (1998). Assuming human males are prone to similar behaviours, dominant men may be more likely to show a preference for women with a restricted sociosexuality. A similar, alternative hypothesis can be generated for the effect of pubertal timing, in that the success of a reproductive strategy to which the acquisition of multiple partners is key could be undermined by the infidelity of those partners.

Based on the above, the following hypotheses are advanced:

1. Early puberty and high dominance in men will be associated with increased preference for femininity in the faces of women.
2. Pubertal timing and dominance will have an effect on male preferences for sociosexuality in the female face.

3.2.4 *Methods*

3.2.5 *Stimulus faces*

Stimulus faces were constructed using the procedure described by Penton Voak et al, 2003 (see also Jones et al, (2007); Buckingham et al., (2006); DeBruine et al., (2006). Faces for this experiment were generated by Boothroyd (2004; 2007). Photographs of the ten highest scorers (most unrestricted) and lowest scorers (most restricted) on the SOI from a sample collected by Boothroyd. (2004; 2007) were converted in to high and low scoring composite images using Psychomorph. Eight base-face composites were constructed using 5 young-adult female individuals in order to generate faces that retain individual identity, yet are 'fictional'. SOI score composites were made from individuals matched for body mass index (BMI). The eight base-faces (5 Caucasian, 1 South East Asian, 1 South Asian and 1 Black) were transformed $\pm 50\%$ of the linear difference in 2D shape and colour between the restricted and unrestricted prototypes using Psychomorph (for technical details see (Rowland & Perrett 1995; Tiddeman et al. 2001)). High and low feminine faces were generated by the same method, using the same 8 base faces transformed $\pm 50\%$ of the linear difference in shape between male and female prototype faces (DeBruine et al., 2006). See figure 3-1 for an example set of stimulus images constructed from one of the Caucasian base-faces.

The same sample of 9, 029 men aged 18-65 as used in Chapter 2 were used for this study. As part of the same, internet based experiment, participants were shown the series of 8 female composite faces

in two conditions; high and low SOI score and high and low feminine. Each transformed pair were presented next to each other. Participants were asked to indicate which face they considered to be more feminine or more interested in casual sex by clicking on an associated 8 point scale that ran from *Guess* to *Extremely more feminine / interested in casual sex* underneath each face. Higher scores for each face indicated preference for femininity or restricted sociosexuality, respectively. Mean preference for femininity and unrestricted sociosexuality across all 8 faces were calculated.

All other variables were assessed and calculated as reported in the previous chapter.

3.2.5.1 Calibration of Face Ratings

The full set of 16 stimulus, female faces were rated on sociosexuality and femininity by a group of independent, online raters attracted to a website from the Perception Lab home page. Participants were shown the full set of 8 faces, transformed to 50% masculine and 50% feminine or 50% more restricted and 50% more unrestricted, presented in a forced choice protocol as in the main experiment. Participants were free to select on which dimension they wished to rate faces and were free to stop after rating one set of faces, consequently sample sizes are different for the two dimensions. The femininity ratings have 606 men and 563 women, while the sociosexuality ratings have 390 men and 693 women. Participants were asked to select which of each image pair looked “more feminine” or “more likely to engage in one-night stands” respectively. Binary choice scores for each face were entered in to separate chi-squared tests, showing that in each of the 8 trials, the 50% feminine transformed face was rated as appearing more feminine at a rate significantly different from chance ($p < .0001$ in each case). Similarly, binary choice scores for the sociosexuality transform indicated that the faces transformed 50% towards unrestricted sociosexuality were consistently rated as appearing more likely to engage in casual sex than the corresponding face transformed 50% towards restricted sociosexuality at a rate greater than chance ($p < .05$ in all cases).

3.3 Results

3.3.1 Preference for Sociosexuality in Female Faces

The data set was split according to age group (18-30 and 31-65, see previous chapter for details). Ranked scores for self-rated attractiveness factor, self-rated dominance factor, relative speed of puberty, Sociosexuality Orientation Inventory (SOI) score and age were entered in to a linear regression (enter method) with preference for sociosexuality as the dependent variable. This produced one significant model for each age group [18-30 year olds: $r^2=.02$, $p<.0001$; 31-65 year olds: $r^2=.01$, $p<.0001$]. Within the younger age group, all independent variables make unique, significant contributions to the model [self-rated attractiveness: $\beta=.08$, $p<.0001$; self-rated dominance: $\beta=.05$, $p=.01$; SOI score: $\beta=.06$, $p<.01$; age: $\beta=.04$, $p=.02$] with the exception of relative puberty speed [$\beta<.01$, $p=.81$], with self rated attractiveness contributing the most. That is, that self-rated attractive, high SOI scoring, dominant, older men show a preference for cues of unrestricted sociosexuality in the face. Among the older men, self rated attractiveness no longer contributes significantly to the model [$\beta=.02$, $p=.21$] while relative puberty speed remains non significant [$\beta<.01$, $p=.99$]. All other variables make unique, significant contributions to the model [self-rated dominance: $\beta=.05$, $p=.02$; age: $\beta=-.05$, $p<.01$; SOI score: $\beta=.04$, $p=.01$], showing that high dominance, high SOI scoring and younger men show a preference for cues of unrestricted sociosexuality in female faces. Dominance and age contribute most to the model. In general, hypothesis 2 is supported, in that high dominance men show an increased preference for cues of unrestricted sociosexuality in the female face. The effect of dominance is independent of self-rated attractiveness. Puberty has no effect in either sample on male preference for sociosexual orientation in female faces, contrary to the hypothesis.

3.3.2 Preference for femininity in female faces.

Identical regressions as reported in the previous section were run with mean femininity preference as the dependent variable. Again, a single significant model was produced for each age group [18-

30: $r^2=.01$, $p<.001$; 31-65: $r^2=.02$, $p<.0001$]. In the 18-30 year old men, only self-rated attractiveness contributes significantly to the model [$\beta=.06$, $p=.001$], suggesting that men who consider themselves attractive prefer more feminine female faces, while no other variable does [self-rated dominance: $\beta=-.02$, $p=.22$; relative puberty speed: $\beta=-.03$, $p=.13$; age: $\beta=.03$, $p=.12$; SOI score: $\beta=.01$, $p=.62$]. Among the 32-65 year old men, self rated attractiveness is not a significant contributor to the model [$\beta=.02$, $p=.23$]. Age is the only significant contributor [$\beta=-.14$, $p<.001$], suggesting older men are less attracted to cues of femininity than younger men, although relative puberty speed approaches significance [$\beta=-.03$, $p=.06$]. Other variables do not make a significant contribution [dominance: $\beta=-.01$, $p=.45$; SOI score: $\beta=.01$, $p=.62$]. Hypothesis 1 is not supported.

3.4 Discussion and Conclusion

There is no support for hypothesis 1, in that neither pubertal timing nor dominance show a relationship with femininity. This may be because, given a straight choice and in the absence of any other cues, all men are likely to choose the most feminine (also likely to be the youngest-looking) face presented to them. Early developing, high dominance men may be less forgiving of low-femininity in a mate and may therefore be more *discriminating*, although there is no evidence for this supposition here. In the current experimental design, which tests for preference for femininity rather than for tolerance of low femininity, all men should be expected to show a preference for high femininity in female faces.

Among the younger men, self rated attractiveness is shown to effect preferences for femininity and cues of unrestricted sociosexuality in the female face. This is in line with the existence of a condition-dependent male mating strategy, influenced by self rated attractiveness as proposed, although not found, by Cornwell et al. (2006), although is not present in the older men, where physical attractiveness may be less important to mate value. Pubertal timing does not show a relationship with preference for sociosexuality in the female face, counter to the hypothesis. Dominance shows a positive relationship with preference for unrestricted sociosexuality in the

female faces, however, suggesting that high dominance men are attracted to cues of sexual accessibility in females. This may facilitate obtaining the maximum number of copulations. This being the case, one would expect a high degree of mate guarding among dominant men, who should be less prone to trust the fidelity of women they have found attractive.

The relationship between male SOI score and preference for cues of unrestricted sociosexuality is evidence for positive assortment on sociosexuality. Although attraction to unrestricted individuals carries with it a high risk of partner infidelity, a man operating a mating strategy where partner numbers are crucial may be expected to preferentially select partners who would be amenable to such a strategy. As before, however, this implies that high SOI scoring men should be expected to demonstrate mate guarding traits (e.g. sexual jealousy) with their long-term partners to a greater extent than low SOI scoring men, who are attracted to more restricted female partners.

Self rated attractiveness is associated with both sociosexuality preference and femininity preference showing a condition-dependent effect on male mate preferences. The results presented here begin to suggest that dominance may play an important role in male mating strategy, independently of other variables. This possibility will receive further attention in the following chapters.

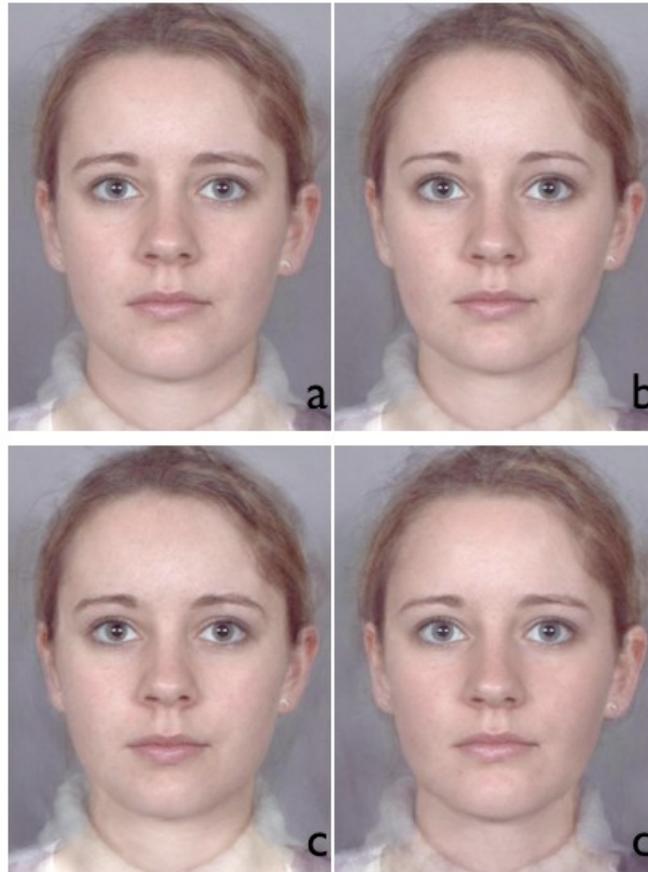


Figure 3-1: Examples of facial stimuli. One of the base-faces transformed to be a) 50% masculine, b) 50% feminine, c) 50% restricted, d) 50% unrestricted (based on SOI score).

4 Pubertal timing, dominance and mating strategy 3: mate preferences.

4.1 Abstract

An alternative measure of mating strategy is to examine the preferred traits of ideal mates. This chapter presents a novel interface for the ranking of traits in an ideal mate, after the work of Buss & Barnes (1986) while testing the hypothesis that early developing men and high dominance men will show exaggerated male-typical mate preferences. Using two, mixed sex samples to identify common mate strategy factors, we establish that men and women consistently differ on the relative ranked positions of kindness and physical attractiveness, with men preferring the latter over the former and women the reverse. Further analysis reveals no relationship between pubertal timing and gender-typical mate preferences among men. Counter to predictions, high dominance men are shown to have increased feminine-typical mate preferences. Combined with the sociosexuality results of the previous chapter, this may indicate a condition-dependent, dual mating strategy in human males, whereby dominant men seek reliable, trustworthy long-term partners while simultaneously seeking multiple, casual-sex relationships with other women. Further results show that earlier developing men across both samples prefer older partners and tolerate a higher age in a partner than later developing men do. This may indicate a positive assortment for sexual maturity.

4.2 Introduction.

Investigations in to human mating strategy have revealed consistent differences between the sexes in emphasis placed on particular traits. A number of investigations into the content of personal, 'lonely-hearts' style advertisements have shown that men place value on traits that link with fertility and fecundity in female partners (attractiveness and youth), while women value traits which reflect an ability to care and provide for them and their children (wealth, status and longevity) (Koziel &

Pawlowski 2003; Pawlowski 1999; Pawlowski & Dunbar 1999) showed that differences in advertised characteristics (rather than desired characteristics) between the sexes also follow identical patterns, with males advertising their wealth and status and females advertising their youth and attractiveness. Buss (1989; Buss & Barnes 1986) have shown, in an analysis of ranked mate preferences in 37 different cultures, that men consistently rank traits related to physical attractiveness higher than women, while women place a greater emphasis on traits related to resource control and status. All of these results are in line with predictions based on evolutionary and parental investment theories, that men seek to maximise offspring number through partner fecundity, fidelity and number, while females seek to maximise offspring quality through the acquisition of a resourceful, supportive partner to provision mother and offspring during development (see Chapter 1).

4.2.1 Speed of Development, Dominance and Mate Preferences

The age at which individual humans go through puberty, as one of a number of life history markers, has been proposed as an adaptively plastic trait which can be adjusted to promote reproductive decisions that reflect optimal allocation of finite energetic, time and resource budgets to reproductive activities within a given environment (Chisholm 1993; Mace 2000; Stearns 1992); this thesis Chapter 1). Individuals developing in a stressful environment should be expected to mature quickly, begin reproduction early and produce a high number of low investment offspring. Those developing in a stable environment with low mortality should be expected to mature slowly, delay first reproduction and produce a small number of higher investment offspring (Black & DeBlassie 1985). The allocation of effort to one path or the other is dependent on the environment in which the individual organism finds itself, and specifically in which it spends its early (childhood) years (Bailey et al. 2000; Belsky 1997; Cornwell et al. 2006b; Moffitt et al. 1992).

Life history markers should be expected to align along a single trajectory (Stearns 1992).

Consequently the life history trajectory which is indicated by speed of development of an individual

should also be apparent in other life history markers and in behaviours related to reproductive tactics. An early developing individual, theoretically operating a 'reproduce early and prolifically' tactic, should also display preferences for partners who best suit the implementation of that tactic. For males, it is likely that this would take the form of an increased preference for partner cues which indicate high fertility and fecundity rather than preferences for wealth or status.

It is a central point of this thesis that increased masculinity should be a consistent feature of early developing male physiology and behaviour, and that, consequently, mating preferences for early developing men may show exaggerated masculine characteristics. Furthermore, resource control, social control and physical prowess are important factors to the attainment of dominance., Consequently the dominance of men, important to their mate-value, should interact with their mating strategy in such a way that high dominant men show an increased preference for high mate-value women, or at least, low dominance men should be realistically seeking lower-mate value women who are likely to be attracted to them. This is based on the tendency of humans to assort for mate value (Buss and Barnes, 1986; Johnstone, 1997). In women, high mate-value should be associated with cues of fertility and fecundity, since these are important features to a man seeking to maximise his offspring number (Thornhill & Gangestad 1999)

The data presented here represents an exploration of a novel interface (the reorderable list) and method for the quantification of mating preferences and in order to test the following hypotheses: Earlier developing and high dominance men will show increased masculine-type preference for partner traits, e.g. higher ranking of traits relating to fertility and fecundity in females.

4.3 Method

4.3.1 Sample 1.

Sample 1 was gathered as an initial test of the reorderable list interface as a viable data gathering method.

A website was constructed and made public via the main Perception Lab site (www.perceptionlab.com). After reading a brief description of the tasks entailed within the experiment and reading a statement of informed consent, participants were directed to a number of linked questionnaire pages. IP addresses were automatically logged and subject codes randomly generated using JavaScript. The questionnaire gathered demographic data on each subject (age, sex, ethnicity, country of residence etc.) as well as age of puberty indexed by retrospective recall of age of first shave (or menarche for female participants) using a drop down menu to select age (including an option for *I have not started shaving/menstruating*) and speed of puberty relative to peers (*Compared to your peers at the time, did you go through puberty... much earlier / much later* on a Likert-type 7 point scale from 1, *much slower*, to 7, *much faster*). Participants were asked to record their sexual orientation on a Kinsey-type scale from 1 (*exclusively homosexual*) to 7 (*exclusively heterosexual*) and to complete the two dominance measures as reported in the previous chapter. Participants were asked to report their own attractiveness (*In general, I consider myself to be ... 1, extremely unattractive* to 7, *extremely attractive*) in order to control for the possible effects of self-rated attractiveness on mating strategy (see Cornwell, 2006). Dominance questions were presented as reported in Chapter 2.

Having answered the demographic questions, participants proceeded to the reorderable, mate preferences list³ (see figure 4-1.). These were presented as lists of mate preference items as per

³ List constructed using open source javascript toolkit: <http://tool-man.org/examples/sorting.html>

Buss & Barnes (1986) although replacing *College Graduate* with *Well Educated* and *Good Heredity* with *Creative*. Each item in the list could be moved vertically in either direction by clicking on it and dragging it in to a new position within the list, using the mouse. Participants were asked to re order the list until it represented the profile of their ideal partner, with *Most Important Trait* at the top and *Least Important Trait* at the bottom. Scores from the list were returned as order of preference, but were converted using Excel in to numerical position for each character trait, giving a score from 1 (*most important in a partner*) to 13 (*least important in a partner*) for each trait.

Participants were asked three further questions relating to the age of their ideal partner. These were selected from drop-down boxes, limited from 17 to 80 years; *What is age of the oldest partner you would tolerate?*, *What is the age of the youngest partner you would tolerate?* and *What is the age of your ideal partner?*

331 individuals from around the world were attracted to the site and completed all tasks. The web data was screened for duplicate ip addresses prior to analysis. The full sample contained 198 women and 133 men, age ranging from 18 to 59 years with a mean age of 26.81 years.

4.3.2 Sample 2.

197 undergraduate psychology students from the University of St Andrews completed task identical to those described for Sample 1. 144 of this sample were female, 53 male. Age ranged from 18 to 39 years with a mean age of 20.24 years (SD=1.97). Sample 2 was gathered to test the replicability of mating preference variables generated in sample 1, confirming the interface as a valid method for investigations of this kind.

4.3.3 Mating preferences

Numerical scores for each mate preference variable from both samples were factor analysed, using varimax rotation. Data from the entire samples were used, irrespective of country of origin. 6

interpretable factors with eigenvalues greater than 1 emerged from sample one, and 6 factors from sample two. Table 1. shows the factor loadings for the highest loading items (>.30) on each factor for both samples as well as percentage variance explained by each factor. Exact (unweighted) factor scores were calculated automatically for each individual.

Item loadings indicate the average relative position of traits compared to each other within in each factor. For example, in Sample 1, Ideal Mate Factor 3 loads positively on *Kind and Understanding* but negatively on *Physically Attractive* and *Exciting*, indicating that the first variable is ranked in opposition to the second two. Since high ranked items score low numbers (the most preferred item scores 1), negative loadings indicate high rankings. Consequently, an individual scoring positively on Ideal Mate Factor 5 ranks *Wants Children* and *Kind and Understanding* higher than the other two items, while a negative score indicates the opposite ranking. .

4.4 Results

4.4.1 Between-sample replication of factors.

The factor loadings for each sample were inspected for similarities. Table 1 shows that in both samples, factors load to indicate negative relationships between relative ranked positions of; *Wants Children* vs. *Intelligent and Well Educated*, *Physically Attractive and Exciting* vs. *Kindness, Good Sense of Humour* vs. *Health*. A further similarity lies in the positive relationship between *Wants Children* and *Religious*. Although there are differences in other factor loadings between the samples, the replication of these specific features in the two samples suggests that the use of the reorderable list followed by factor analysis of results as a method for the assessment of variation in mating strategy.

In both samples, the *Physically Attractive and Exciting* vs. *Kind and Understanding* (and *Wants Children* in sample 2) factor (factor 3 in both samples) shows a sex difference in that mean scores for men in both samples are higher than for women [sample 1: $t(194)=-3.09$, $p=.002$; sample 2:

$t(118.4)=-3.041, p=.003]$, indicating that males rank physical attractiveness higher than kindness as an ideal partner trait, while females do the opposite. This sex difference is in line with predictions on male and female mating strategy based on differences in obligatory investment in offspring. It is of particular interest that factor 3 in sample 2 places attractiveness and excitement in opposition to kindness and desire for children, for this is precisely the sex difference that evolutionary theories of human mating strategy would predict. In sample 1, factor 5 (*Easygoing* and *Creative* vs. *Earning Capacity* and *Wants Children*) also shows a sex difference [$t(180.54)=-2.12, p=.04$, assumption of equal variances violated, $F=7.19, p=.01$]. Various factors in sample 2 show further sex differences, see Table 2 for a summary of these.

These data replicate the findings reported by Buss and Barnes (1986) that men value physical attractiveness more highly than women do and demonstrates the validity of the computer-based, reorderable list as a valid method for generating mate-preference information. Sample 2 shows further sex differences which are not apparent in sample 1. For a summary of these, see table 4.2.

4.4.2 *Mating Preferences and Pubertal Timing*

Sub-samples of male, heterosexual Caucasians were extracted from each sample. Sample 1 was further limited to the same age range as present in sample 2 (18-39 years). This left sample sizes of 69 males in sample 1 and 44 males in sample 2. 19 individuals failed to complete the mate preferences tasks in sample 1. They are necessarily excluded from analysis of mate preference factors, further reducing sample 1 to 50 individuals.

4.4.3 *Dominance score*

Social and physical dominance measures were combined using factor analysis of respective questions, both loading on a single factor accounting for 84.04% of total variance in sample 1 and 65.04% of the variance in factor 2. See table 3 for loading summary.

4.4.4 Sample 1 (Web-based sample)

All variables were rank transformed prior to regression analysis.

Two multiple linear regressions (enter method) were run, with age of puberty and relative puberty speed as respective dependent variables. Independent variables were rank transformed age, self-rated attractiveness and all 6 mate preference factors. This failed to produce a significant model for either puberty variable [age at first shave: $F=.41$, $df=8$, $p=.91$; puberty speed: $F=1.31$, $df=8$, $p=.27$]. Regressing the same variables against rank of dominance factor score produces a model which approaches significance [$F=2.13$, $df=8$, $p=.06$] in which only rank of self-rated attractiveness makes a near-significant contribution [$\beta=.29$, $p=.05$].

Spearman's rank order correlations on untransformed variables show that minimum, maximum and ideal partner age do not correlate with age of first shave [minimum partner age: $r=-.19$, $n=44$, $p=.21$; maximum partner age: $r=-.09$, $n=44$, $p=.56$; ideal partner age: $r=-.16$, $n=44$, $p=.29$]. Relative puberty speed correlates positively with maximum partner age [$r=.37$, $n=44$, $p=.01$] and shows a positive trend with ideal partner age [$r=.26$, $n=44$, $p=.08$], but does not correlate with minimum partner age [$r=-.24$, $n=44$, $p=.21$], suggesting that early developing males tolerate older partners than later developing males. Dominance factor score correlates with maximum partner age [$r=.39$, $n=46$, $p=.01$] but not with minimum partner age [$r=.23$, $n=46$, $p=.13$] or ideal partner age [$r=.23$, $n=46$, $p=.13$].

4.4.5 Sample 2 (undergraduate sample)

All variables were rank transformed prior to regression analysis.

Rank transformed age, self-rated attractiveness and all mate-preference factors were entered in to a linear regression analysis (enter method) with, respectively, rank of puberty speed and rank of age of first shave as dependent variables. Neither analysis produces a significant model [relative speed of puberty: $F=.52$, $df=8$, $p=.83$; age of first shave: $F=1.49$, $df=8$, $p=.20$].

A further regression was run (enter method) with rank of dominance factor score as the dependent variable and all other independent variables the same. This produced a significant model [$F=5.43$, $df=8$, $p<.0001$]. Mate factors 1 [$\beta=-.42$, $p=.01$], 2 [$\beta=-.40$, $p=.01$], 5 [$\beta=-.38$, $p=.01$] and 6 [$\beta=.53$, $p<.001$] all make unique, significant contributions to the model, as does self-rated attractiveness [$\beta=.36$, $p=.01$]. These results suggest that high dominance men tend to rate, respectively, *Well Educated* and *Intelligent* over *Wants Children* and *Exciting*; *Good Earning Capacity* and *Good Sense of Humour* over *Creative*; *Good Earning Capacity* and *Healthy* over *Easygoing* and *Good Sense of Humour*; and *Religious* over *Good Housekeeper*. Factor 6 (*Religious* vs. *Good Housekeeper*) makes the largest contribution. No other variable contributes significantly.

Spearman's rank order correlations on untransformed variables show that ideal partner age correlates negatively with age of first shave [$r=-.32$, $n=41$, $p=.04$] and positively with speed of puberty [$r=.44$, $n=41$, $p=.004$]. Maximum partner age also correlates positively with puberty speed [$r=.43$, $n=41$, $p=.006$], showing that early developing males in this sample prefer and tolerate older partners than late developing males. None of the partner age variables correlate with dominance factor score [ideal partner age: $r=.06$, $n=40$, $p=.72$; minimum partner age: $r=.06$, $n=42$, $p=.71$; maximum partner age: $r=.17$, $n=42$, $p=.29$]

4.5 Discussion

The hypothesis that men reporting early puberty will display increased male-typical mate preferences compared to later developing men is not supported by this data. Neither age of first shave nor relative speed of puberty have a significant relationship with any of the mate preference factors.

While high dominance has an effect on mate preference factors in the second, undergraduate sample (*Creative* vs. *Good Sense of Humour* and *Religious* vs. *Housekeeper*), there is no significant effect of dominance on mate preferences in the internet-based sample. The lack of replication for the

mate preference effect across the two samples may be due to a higher degree of homogeneity in the second, undergraduate sample than in the first. The students making up sample 2 are likely to be of similar socioeconomic brackets, while the internet-gathered sample 1 may have greater socioeconomic variance. High socioeconomic status has been reported to have a negative relationship with speed of maturity in many human societies (see Mace, 2000 for review) and may have effects on mating strategy and partner preferences as well (Belsky et al. 1991). Furthermore, although all participants included in the subsample of sample 1 were Caucasian, participants reported a wide range of countries of residence, whereas most participants of sample 2 were members of the same community. Resulting cultural differences may have further effects on mate preferences (Buss & Barnes 1986).

Although male dominance is shown to effect the score of sex-differentiated mate preference factors in Sample 2, the effect is in the opposite direction from that predicted: high dominance men appear to be behaving in an increased feminine-typical manner, preferring, *Good Earning Capacity* and *Good Sense of Humour* over *Creativity*; *Good Earning Capacity* and *Health* over *Good Sense of Humour* and *Easygoing*; and *Religious* over *Good Housekeeper*. These preferences are generally female typical within the sample as a whole (see table 2). As a consequence, the hypothesis that increased dominance would be associated with increased male-typical mate preferences is not supported. This is an unexpected result, particularly given the tendency of high dominance men to report unrestricted sociosexuality (see Chapter 3), which is a stereotypically masculine trait. In fact, the coupling of unrestricted sociosexuality with a decreased preference for physical attractiveness in a partner seems counterintuitive, since a mating strategy emphasising offspring number over offspring quality (a short term, unrestricted sociosexuality strategy) should be associated with a preference for physical cues of fertility and fecundity.

Work on the mating strategy of women has shown that human females operate a condition dependent 'dual mating strategy' in that a woman's mating preferences shift according to menstrual

condition and relationship status in ways consistent with the hypothetical female drive to find the best possible genetic father for her children as well as the best carer for those children (given that these may be two different men). Beyond the work of Cornwell et al.(2006) and Little et al. (Unpublished), where self-rated attractiveness was proposed as a condition on which male mating strategy depends, very little work has been advanced on a male condition dependence in mating strategy. There is a suggestion here, however, that male mating strategy may, in fact, depend on self assessment of dominance, and does so independently of self-rated attractiveness. High dominance men, given their unrestricted sociosexuality, should show a tendency to engage in multiple, short term relationships, yet show relationship preferences which do not tally with this tendency, albeit in only one of two samples presented here. The mate preference task is presented in terms of ideal partner choice which may, although no specific instructions exist to that effect, predispose an individual to approach the task with a long-term relationships in mind (the word “ideal” could potentially bias a task in this regard, since ideal partners are, traditionally, long term partners). If this is the case, then there is also potential that these results suggest the presence of a dual male mating strategy whereby the ideal (i.e. long-term) partner is chosen on her ability to raise and care for children (*wants children*), while the unrestricted sociosexuality of the high dominance male predisposes him to seek extra pair copulations with other women. This would be an ideal situation for a male, since he would have a number of offspring with a long-term partner in whom he would be obliged to invest (high quality offspring) whilst maintaining the possibility to produce high numbers of low investment offspring at the same time. Successful implementation of this strategy requires not only that a male control sufficient resources, but also that he be attractive to women. Both of these features are connected to his dominance and would imply that a man operating this proposed dual strategy should be high in dominance.

In the first, web-based sample high dominance men show a higher tolerance for older partners than low dominance men, although there is no relationship between dominance and ideal or minimum

partner age and the effect is not replicated in the undergraduate sample. By contrast, both samples show a relationship between puberty variables and partner age. While there is no difference in the minimum age of preferred partner (which might be expected, given the general tendency of men in general to find youth attractive (Jones 1996; Symons 1979; Thornhill & Gangestad 1999); earlier developing men report a preference for older ideal partners as well as an increased tolerance for age in their partners (higher maximum age of partner). This may be due to the fact that, at the point at which they entered the sexual arena, early developing men would be more likely to be assorting with sexually mature women who may either be or appear to be older than their peer group (positive assortment for sexual maturity). This may lead to a preference for slightly older women which would track through life, or at least through early adulthood.

It is, of course, possible that the addition of further mate preferences to the list or the replacement with another set of mate preference traits may reveal more differences in mating strategy between early and late developing males. The traits presented here, however, have for the most part been validated as traits valued by humans, albeit to different extents, cross culturally and should be expected to expose differences in mating strategy, if differences exist (Buss 1989; Buss & Barnes 1986). Given that men and women show predicted sex differences in their preferences in the data presented here, the novel, reorderable list interface and factor analysis of results has been validated as a method for investigations of this kind.

4.6 Conclusion

While early development is not associated with any difference in mate preferences, counter to predictions, high dominance is associated with an increased femininity of mate characteristic preferences. This, combined with the results from the previous chapter showing high dominance is associated with unrestricted sociosexuality, may suggest the existence of a male dual mating strategy which is dependent on dominance. Given that this effect is not replicated, the possibility remains speculative, although the identification of a potential condition-dependent mating strategy

in human males is certainly worthy of further attention. Men reporting earlier puberty also show a tendency to prefer and tolerate older partners than later developing men, possibly as the result of a positive assortment for maturity. The results presented here also validate a novel method for the quantification of mate preferences.

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RATINGS 1.

PARTNER PREFERENCES.

TASK: Look at the list below.

Please arrange the items in the list below in to order of most important to least important feature when considering your ideal partner .

To move an item, click on it and drag it in to a new position.

MOST IMPORTANT IN A PARTNER

Kind and understanding
Exciting Personality
Intelligent
Physically Attractive
Healthy
Easygoing
Creative
Wants children
Well educated
Good earning capacity
Good sense of humour
Good housekeeper
Religious

LEAST IMPORTANT IN A PARTNER

CONTINUE

Done

Figure 4-1: The reorderable list and mate preference traits. Items in the list can be dragged vertically in to new positions by clicking on an individual box and moving it using the mouse

	<i>Sample 1 (web based)</i>					
	<i>Mate Preferences</i>					
<i>Factor</i>	1	2	3	4	5	6
<i>(variance explained)</i>	14.8%	12.8%	12.0%	9.9%	9.4%	7.7%
<i>Eeasygoing</i>					-0.39	0.60
<i>GSOH</i>		-0.71		0.43		
<i>Children</i>	-0.56				0.46	
<i>Exciting</i>			-0.53	-0.64		
<i>Creative</i>	0.30			-0.40	-0.57	
<i>Kind</i>	-0.33	0.57	0.32			
<i>Healthy</i>		0.76				
<i>Good_earner</i>					0.77	
<i>Housekeeper</i>				0.78		
<i>Religious</i>						-0.87
<i>Well_educated</i>	0.71					
<i>Intelligent</i>	0.68					
<i>Physically_attractive</i>			-0.87			
	<i>Sample 2 (Undergraduate)</i>					
	<i>Mate Preferences</i>					
<i>Factor</i>	1	2	3	4	5	6
<i>(variance explained)</i>	13.6%	12.4%	11.6%	10.3%	9.2%	8.0%
<i>Eeasygoing</i>					-0.67	
<i>GSOH</i>		0.46		0.53	-0.37	
<i>Children</i>	-0.36			-0.73		
<i>Exciting</i>	-0.41		-0.39	0.46		
<i>Creative</i>		-0.77				
<i>Kind</i>			0.63			
<i>Healthy</i>					0.74	
<i>Good_earner</i>		0.67			0.33	
<i>Housekeeper</i>						0.77
<i>Religious</i>				-0.43		-0.58
<i>Well_educated</i>	0.77					
<i>Intelligent</i>	0.71					
<i>Physically_attractive</i>			-0.82			

Table 4-1: Factor loadings and percentage variance explained for ranked ideal mate traits for both samples. Colours indicate common factors between the samples. Yellow: Wants Children vs Intelligent and Well Educated; Blue: Good Sense of Humour vs Health; Red: Physically Attractive and Exciting vs Kind and Understanding; Green: Creative vs Good Sense of Humour

	<i>t</i>	<i>df</i>	<i>Sig.</i>	<i>Females prefer</i>	<i>Males prefer</i>
<i>Wants Children & Exciting vs Well Educated & Intelligent</i>	0.48	185.0	0.628	Wants Children & Exciting	Well Educated & Intelligent
<i>Creative vs Good Earning Capacity & Good Sense of Humour</i>	-3.77	185.0	0.000	Good Earning Capacity & Good Sense of Humour	Creative
<i>Physically Attractive & Exciting vs Kind and Understanding</i>	-3.04	118.4	0.003	Kind and Understanding	Physically Attractive & Exciting
<i>Wants Children & Religious vs Good Sense of Humour & Exciting</i>	-1.27	185.0	0.204	Good Sense of Humour & Exciting	Wants Children & Religious
<i>Good Sense of Humour & Easygoing vs Good Earning Capacity & Health</i>	-0.39	185.0	0.701	Good Earning Capacity & Health	Good sense of Humour & Easygoing
<i>Religious vs Good Housekeeper</i>	4.06	185.0	0.000	Religious	Good Housekeeper

Table 4-2: differences in ideal mate preference factors from Sample 2 (undergraduates).

5 Sensitivity to pheromones as an indicator of reproductive strategy: the effect of pubertal timing and self-rated dominance.

5.1 Abstract

Both pubertal timing and dominance should impact on response to reproductively relevant signals as part of a larger impact on mating strategy. This possibility is examined in a sample of 57 adult men, using self reported pubertal timing and social dominance data and the putative male pheromones 4,16-androstadien-3-one,5 α -androst-16-en-3-one and the putative female pheromone 1,3,5(10),16-estratetraen-3-ol. Alternative hypotheses are advanced regarding male detection of the putative female pheromone that subdominant males or dominant males will be better at detecting the odorant, contingent on whether the compound signals ovulation or pregnancy respectively. A further hypothesis is advanced that early developing males will be more sensitive to all pheromones, reflecting the greater interest in the fertility of women that their mating strategy ('reproduce early-reproduce often') should emphasise. Results give no support for the puberty hypothesis, but provide support for the hypothesis that high dominance males will be more sensitive to female odorants. Further support for the suggestion that high dominance males are responding to a pregnancy cue in order to avoid non-fertile matings is shown in a second sample of 49 adult males, where self-rated competitiveness is shown to correlate negatively with attraction to the compound. Results are discussed in terms of the evolution of mating strategies in anthropoid primates in general.

5.2 Introduction

This chapter presents a study of sensitivity and attitudes towards putative human pheromones as potential indicators of reproductive condition. Differences in sensitivity or reaction to sexually relevant signals may indicate differences in mating strategy between low and high dominance men or early or late developing men. First, the relevant literature concerning pheromones and their relationship to mating strategies are reviewed.

5.2.1 Pheromones

The term ‘pheromone’ was first introduced by (Karlson & Luscher 1959), the same year as the first pheromone, Bombykol, was identified in the female silk moth *Bombyx mori*, by (Butenandt et al. 1959). Pheromones are “airborne chemical signals that are released by an individual into the environment and which affect the physiology or behaviour or other members of the same species” (Stern & McClintock 1998). Most animal species have been reported as producing and responding to pheromones under a variety of conditions.

Although associated most commonly with mating behaviour, pheromones have also been linked, in mammals, with alarm / fear responses in mice (Rottman & Snowdon 1972) with nipple-search in suckling rabbit young (Hudson & Distel 1995) and with approach/avoidance behaviours (Chen & Haviland-Jones 1999). Pheromones have also been associated with reproductive activity and with oestrus synchrony in domestic mammals (McClintock 1981) and in humans (Stern & McClintock 1998). Broadly, pheromones are a class of air (or water) borne biostimulants. It should be immediately noted that the production and detection of pheromones by humans has been a hotly debated topic for some years, with many researchers strongly doubting that human pheromones exist at all (see Wysocki & Preti (2004) for review.

Nevertheless, experimental work has shown that humans are at least capable of producing pheromones and appear to respond to them (see below).

Biostimulation, referring to the ability of signals produced in any sensory modality by one animal to have an effect on the physiology and/or behaviour of another of the same species, has been repeatedly shown to be important in animal reproduction (Brennan & Keverne 2004; Rekwot et al. 2001). The ability of one animal to assess the reproductive condition of a conspecific from communications offered by that conspecific is extremely important to the implementation of a successful mating strategy in terms of identifying appropriate targets for mating attempts. If individuals are providing information which can be decoded into indicators of reproductive condition, then evolutionary theory predicts that other, interested animals (i.e. those seeking potential mates) should evolve mechanisms for the exploitation of those signals. Pheromones have been identified as one mechanism by which mammals can communicate reproductive condition to others (Powers & Winans 1975; Rekwot et al. 2001; Singer & Macrides 1990; Wysocki et al. 1982). Biostimulation by pheromones has been well used in the animal husbandry industry to promote the breeding of domestic animals (Burns & Spitzer 1992; Rekwot et al. 2001) .

Pheromones are used extensively by insects to identify kin (wasps, Gamboa (1996), to signal immunocompetence (grain beetles, (Rantala et al. 2002; Rantala et al. 2003) and dominance (cockroaches, Roux et al. (2002) and to manipulate the physiology and behaviour of conspecifics (queen ants, Dawkins (1986)). Insect pheromones are chemically distinct from mammalian, the only similarity lying in the purposes to which they are put, although in both orders pheromones are volatile compounds secreted by the organism (Singer & Macrides 1990). While insects metabolise and release pheromones as gaseous compounds, mammals lace other bodily secretions (for example saliva, apocrine secretions or urine) with the chemical signals (Pawlowski 1999) and release them in to the air. As

volatile chemical compounds, some pheromones must bind to a large and well-known family of water-binding proteins called lipocalins (lipocalycins) in order to be transported in such aqueous media (Brennan & Keverne 2004). The lipocalins themselves, which have well-reported odour-binding effects (Singer 1991) and are often found in olfactory epithelia as part of the mammalian chemosensory system (Brennan & Keverne 2004), may also act, in some instances, as biostimulants. The lipocalin Aphrodisin is found in vaginal secretions of the golden hamster *Mesocricetus auratus* and is known to indicate estrus and attract male hamsters, although whether it performs this function in itself or as the binder for an as yet unidentified pheromone is unknown (Brennan & Keverne 2004; Singer 1991; Singer & Macrides 1990).

5.2.2 Pheromones in humans.

Even though humans, compared to other mammals, have fewer receptor cells for olfactory communication, they produce the greatest quantity of olfactory substances of all the primates, having more and larger sebaceous and apocrine glands than the rest of the order (Stoddart 1990). Most pheromones are produced by the action of aerobic coryneform bacteria on the surface of the skin as they metabolise androgenic and other hormonal compounds (Mallet et al. 1991), the products of which are dissolved in watery secretions of the eccrine glands (Pawlowski 1999). As Stoddart (1990); see also Pawlowski (1999) observes, the presence of hair surrounding the location of most apocrine and eccrine (sweat producing) glands (e.g., armpits, ano-genital region) is unlikely to be an adaptation towards heat conductance since these areas are generally 'closed'. Rather, the hair may provide a greater surface area for the action of pheromone-producing microorganisms and for the diffusion of their metabolites (Pawlowski 1999).

The fact that humans appear well adapted for the production of odourants is grounds to predict that mechanisms for the detection of odourants should also be present in humans. Other mammals which routinely use pheromonal communication use the Vomeronasal Organ (VNO) for this purpose (Doving & Trottier 1998; Keverne 1999; Powers & Winans 1975). The Vomeronasal system, also called the accessory olfactory system, is distinct from the main olfactory system and is believed to be used by most mammals specifically to detect and assess specific types of odourants not detected by the main olfactory system, odourants that are associated mainly with social interactions and, most typically, with mating; these being pheromones (Moran et al. 1991; Wysocki et al. 1982). Whether or not the VNO exists in humans has been the subject of some debate, despite the fact that the absence of the VNO is routinely cited as a diagnostic synapomorphy of the entire catarrhine sub-order of primates, of which humans are a member (Bhatnagar & Meisamimi 1998; Smith et al. 2001). There is, however, a growing body of work suggesting that the VNO is more common in the “higher” orders of primates, including humans, than previously thought (Smith et al. 2001)).

Investigations of human nasal anatomy have lead to variable results. Examining human nasal mucosa in live subjects during routine plastic surgery revealed the presence of VNO in 808 out of 1000 patients (Garcia-Velasco & Mondragon 1991), while a similar study conducted by Won et al. (2000) revealed the presence of openings leading to a Vomeronasal Duct in 28.2% of live humans but 59.1% of cadavers, this disparity due to ease of dissection of the nasal mucosa in the dead that is not possible in the living. Kreutzer & Jafek (1980) have found prenatal evidence for a human VNO in embryos and fetuses, although the accessory olfactory nerves degrade after birth (Witt et al. 2002). Moran et al., (1991), p546) report that, while examinations with the naked eye reveal the VNO in 10% of subjects, the proportion of individuals in which “paired, bilateral pits”, indicating the presence of the VNO, are detected rises to 100% when a microscope is used, and Stensaas et al., (1991) find

a VNO in 100% of 410 examined subjects. Moran et al., (1991) go on to report finding evidence for a VNO in over 200 subjects of all ages and sex. While Garcia-Velasco & Mondragon (1991) are content to take the presence of openings in the nasal mucosa as indicative of a VNO identical to that in other mammals, other researchers are more restrained. Since the openings lead to a duct which varies in length from 2 to 7mm in length, terminating in a blind “pouch” (Garcia-Velasco & Mondragon 1991), the putative human VNO is much smaller than that of other mammals, an observation which, coupled with the observed variation in length of the duct and its total absence in some humans, has led Knecht et al. (2001) to suggest that the VNO is a vestigial structure and is potentially, as such, no longer functional. Knecht goes further and suggests that the human VNO is so structurally different from that of other animals that it should be renamed the Vomeronasal Duct (VND). Vestigial or not, there is some evidence that the human VNO is functional. Exposure to putative pheromones causes significant electrical potential fluctuations in the VNO, suggesting that the organ is functional and, moreover, has specific receptor sites for pheromones (Monti-Bloch & Glosser 1991).

Even without a VNO, some research suggests that humans would be able to detect pheromones. While rodents detect and process pheromonal system using their VNO, the domestic goat has two systems capable of pheromone detection. Wakayabashi et al. (2002) isolated the VR1 genes used in both rodents and goats to detect pheromones in the VNO, and found the same genes present in the olfactory epithelium (part of the main olfactory system) of goats, suggesting that both olfactory systems respond to pheromones in these animals. The VR1 genes are also present in the human olfactory epithelium (Rodriguez et al. 2000) which leads to a tentative conclusion that humans too may have two systems capable of pheromone detection, and that even those humans wholly lacking a VNO may be able to detect pheromones through the olfactory epithelium. However, both Giorgi et al. (2000) and

Kouros-Mehr et al. (2001) assert that the human VR1 genes are non-functional pseudogenes.

Cranial nerve zero (*nervus terminalus*) runs from the frontal lobe of the brain to the nasal cavity and has been put forward as being part of a secondary olfactory system specifically geared towards the detection of pheromones. The existence of cranial nerve zero as a distinct cranial nerve has been debated, with some researchers suggesting that potential examples of the nerve in dissected animal brains are, in fact, frayed ends of cranial nerve one, the main olfactory nerve and that the nerve, if it exists at all, may not serve any function beyond that of cranial nerve one. Recent dissection of pilot whale brains, which have no sense of smell, support the claim that cranial nerve zero exists as an anatomical feature, with a distinct function from the main olfactory nerve (Fields 2007). Experiments on rodents and fish have shown that cranial nerve zero is crucial to arousal and mating behaviour (see Fields (2007), for review). Dissections of human brains have shown, as expected, that humans do possess a cranial nerve zero, which, as part of the accessory olfactory system (the VNO) is further evidence that humans are capable of detecting pheromones.

5.2.2.1 *Experimental responses to pheromones in humans.*

Further evidence that humans have an ability to detect pheromones comes from the effects that pheromones can have on humans. Most famously, Stern & McClintock (1998) used female axillary secretions to synchronise the menstrual cycles of unrelated female humans. Benton (1982) reports that females asked to wear a male pheromone on their upper lip every night for a month report themselves as being more submissive when mid-cycle. Pause (2004), in a replication of Kirk-Smith et al. (1978), demonstrated that female subjects will

preferentially sit in a chair in a waiting room treated with male pheromone, androstadien, and that males will avoid a lavatory cubicle treated similarly.

Evidence that pheromonal signals may contain information relevant to the human mating arena comes from a number of experiments that show individuals responding to opposite-sex associated pheromones. Human females have reported greater increase in confidence with opposite sex interaction after sleeping with a pendant treated with male pheromones around their necks, although no increase in sexual desire or activity (Cowley & Brooksbank 1991) while Chen & Haviland-Jones (1999) report that both sexes show a decrease in depressive mood two minutes after exposure to the underarm odour of either sex. Savic et al. (2001) showed that the hypothalamus of the heterosexual female brain activates when smelling androgen-based odourants, while the heterosexual male hypothalamus activates in response to estrogen-like substances. Recently Savic et al. (2005) have showed that the brains of homosexual men respond to male pheromones in the same way as heterosexual women. Bensafi et al. (2004) exposed volunteers to male and female pheromones while exposing them to either 'sexually-arousing', 'sad' or 'happy' film segments, as well as a neutral control condition. Participants showed no autonomic or behavioural changes during the neutral condition, but showed increased sexual arousal and skin temperature during the sexually arousing contexts when exposed to putative pheromones of either sex (males also displayed a slowed respiration rate). The same research shows that exposure to male pheromones maintains positive mood in females during the sad context, but increases negative mood in males.

Response to pheromones may also indicate details of individual variation in mating strategy. Cornwell et al. (2004) showed that female preferences for masculinised male faces correlate positively with female preferences for male pheromone androstadien. Male preferences for feminised female faces correlate positively with their ratings of female pheromone

estratetraen, suggesting the use of concordant signals from multiple sensory modalities in the assessment of a mate. Repeated investigations have shown that facial preferences can be modified by the application of opposite sex pheromones, and that females can be induced to rate male faces as being more attractive when exposed to androgen-like pheromones Cowley & Brooksbank (1991; Filsinger et al. 1984; Kirk-Smith et al. 1978; Thorne et al. 2002) and Filsinger et al. (1990) find that males show a tendency to rate other males more negatively during exposure. Overall, there is substantial evidence that humans can detect pheromones and that they are strongly linked with mate identification, assessments of attractiveness and mating behaviour.

Although it is as yet uncertain whether humans *produce* pheromones and, if so, what it is that humans use pheromones to communicate, it seems a reasonable conclusion, given the above evidence, that humans can *detect* pheromones and that they have a number of effects, mainly linked with the sexual arena.

As putative sexually-relevant signals, pheromones may be influenced by factors linked to mating strategy and preferences (Cornwell et al. 2004). In particular, there are grounds for supposing that dominance and pubertal timing may influence pheromone detection.

5.3 *Pheromones and dominance.*

If female ovulation is communicated by pheromones, then they are ideal substances with which to test the hypothesis from Chapter 3 that dominant men will be more sensitive to cues of female fertility than subdominants. There is evidence that human males prefer the scent of ovulating women to that of women at other stages of their menstrual cycle (Poran 1994; Singh & Bronstad

2001) which certainly suggests that reproductive condition may be communicated through odorous cues in women, although as yet no evidence to link a pheromone to this effect.

One putative female mammalian pheromone, 1,3,5(10),16-estratetraen-3-ol (estratetraen), is an oestrogen metabolite (Laska et al. 2006), so should be expected to peak in production when oestrogen levels are highest; around ovulation. Estratetraen has to date only been reported in the urine of pregnant women (Thysen et al. 1968), which suggests it may not signal ovulation in human females, unless further work reveals another source of the compound.

In many anthropoid primate groups, females demonstrate false estrus during pregnancy and many male conspecifics respond to such pseudo-estrus by attempting copulations in the same way as if the female were cycling normally (Engelhardt et al. 2007; Gordon et al. 1991; Gortitze 1996; Manson et al. 1997). The males' apparent lack of ability to differentiate between normally cycling and pregnant females has been proposed as a mechanism by which a female can confuse paternity of her offspring and thereby avoid infanticide of her offspring. Researchers have noted, however, that alpha males do not attempt copulation with pregnant females and appear to be the only males who are not fooled by the pseudo-oestrus (Engelhardt et al. 2007; Gordon et al. 1991). This may be due to the increased exposure to females the dominants have when they are in estrus (Pradhan et al. 2006), meaning that extra copulations with non-fertile females is a waste of energy that subdominants, who have less access to estrus females, should be willing to expend on the slight chance that conception will result from a copulation. The mechanism by which dominants are able to detect pseudo-estrus is unknown, although Engelhardt et al. (2007) suggest the phenomenon may be mediated by pheromones.

Based on the above, two alternative hypotheses are advanced, each contingent on the information being signaled by putative female pheromones:

either

1. Subdominant men will be more sensitive to the putative female pheromone estratetraen as a pheromonal cue of female condition and fertility as part of a subdominant mating strategy.

or

2. Dominant males will be more sensitive to the putative female pheromone estratetraen (as a pheromonal cue of pregnancy) as part of an anthropoid mechanism to avoid non-fertile matings with pregnant females.

No specific predictions are made for a relationship between dominance and detection of putative male pheromones.

5.4 *Puberty and Pheromones*

Early puberty in men may be an indicator of their placement on a developmental trajectory that emphasises early and prolific reproduction (Chisholm 1993; Stearns 1992; Stearns 2000). Early developing males have been shown have a more unrestricted sociosexuality (Chapter 2) and were predicted as being likely to show increased preferences for cues relating to fertility and fecundity in women (youth / health). This was not found during the investigation in to female face preferences in Chapter 3. Here the prediction is tested again in a separate modality. Regardless of whether the compound estratetraen signals ovulation or pregnancy, early developing males should be expected to be more sensitive to it as a signal of reproductive condition and, hence, fertility. Furthermore, although the putative pheromones 4,16-androstadien-3-one and 5 α -androst-16-en-3-one are classified as 'male', they are produced by both sexes. As testosterone metabolites, they should be dependent on individual differences in testosterone levels. There is some evidence that women

displaying unrestricted sociosexuality (a greater than average interest in casual sex) are more masculine (Mikach & Bailey 1999), a phenomenon which may be due to higher levels of testosterone in those women. Men operating a 'reproduce early-reproduce often' strategy should be attracted to women showing interest in casual sex and attentive to any cue which advertises that status.

Based on this, a third hypothesis is advanced;

3. Early developing males should be more sensitive to all putative mammalian pheromones.

5.5 *Materials*

Three putative human pheromones were used. Two 'male' associated: 4,16-androstadien-3-one and 5 α -androst-16-en-3-one (for brevity, henceforth referred to as AND1 and AND2, respectively) and one female associated 1,3,5(10),16-estratetraen-3-ol (henceforth EST). All pheromones were supplied by Steraloids Inc. (RI, USA). Solutions were made at a concentration of 2mg per 1.0ml of propylene glycol, 200 μ l of which was deposited by micro-pipette on to filter paper and placed in to clear glass bottles (after Cornwell et al. 2004). Each bottle was sealed with a plastic cap. When not in use, the pheromones were stored at a temperature of 5° Celsius and were allowed to come up to room temperature for half an hour before use in experiments.

5.6 *Methods*

57 men [mean age 20.9 years, SE=1.46, range from 18 to 25 years] were recruited from the undergraduate population of the University of St Andrews and completed all tasks in laboratory conditions. All participants attended testing sessions on two occasions. On their first visit, they answered questionnaires, completed the pheromone detection task and gave a saliva sample (see

below) for hormonal assay. On their second visit they gave a second saliva sample, were debriefed and paid. Ethical approval was given by the University of St Andrews ethical committee.

5.6.1 Pheromone detection.

Pheromones were presented in three sets of three bottles each. In each set, one bottle contained a pheromone, the other two were blanks. A further condition containing an oil of cloves stimulus (at the same concentration as the pheromones) was presented to test for general anosmia. Participants were asked to identify, in each set of 3 bottles, which bottle contained a scent by indicating their choice on a computerised score sheet. Bottles were identified using single letters. The 4 sets of 3 bottles were presented in random order, automatically allocated by html.

5.6.2 Questionnaire

General demographic, age and sexuality data was gathered as per previous experiments. Puberty questions as detailed in earlier chapters were presented to assess age of first shave and relative puberty speed.

A 5 item dominance inventory as presented in the IPIP (<http://ipip.ori.org/ipip>) (Goldberg 1999; Havlicek et al. 2005) was presented to each participant. The questions in the scale, (on a 7 point scale from 1, *not at all like me*, to 7, *very much like me*) were: *I often try to surpass others' accomplishments; try to outdo others; am quick to correct others; impose my will on others; demand explanations from others; want to control the conversation; am not afraid of providing criticism; challenge others' points of view; lay down the law to others; put people under pressure* and a negative keyed *hate to seem pushy*. These questions are generally slanted towards group influence and popularity, and form a measure of human dominance within the social arena.

5.7 Results

5 males were excluded from analysis on the basis of their BMI (Body Mass Index) being over 30 kg/m² ('obese' according to BMI guidelines). BMI was calculated by dividing each participants weight by their height squared. BMI is known to have a relationship with pubertal timing in women (Kaplowitz et al. 2001) and may lead to unusual hormonal conditions in both sexes. For this reasons, only people scoring below 30 kg/m² were included in analysis. The oil of cloves stimulus was included to provide a baseline olfaction measure and to exclude anosmics. 100% of the participants could identify the target bottle in this condition, however, so no exclusions were made on this basis. The final sample therefore contains 52 participants. One male did not answer the relative pubertal timing question, so the sample drops to 51 for this variable.

5.7.1 Dominance and pheromone detection

Participants were split on the median of the dominance inventory score [median = 31.8]. Those scoring lower than the median [n= 26] were classified as low dominance. Those scoring higher were classified as high dominance [n=26]. Further groups were calculated for the detection of pheromones based on their ability to correctly identify the stimulus bottle [AND 1 detectors n=29, AND 2 detectors n =27, EST detectors n=19]. Chi squared tests show that subdominant men are less likely to detect EST, the female pheromone, than dominant men [$\chi^2 = 4.06$, $df=1$, $p=.04$, see figure 5-1]. There is no significant effect of dominance on ability to detect the two putative male pheromones [AND1 $\chi^2 = .08$, $df=1$, $p=.78$; AND2 $\chi^2 = .08$, $df=1$, $p=.78$].

5.7.2 Puberty and pheromone detection.

Participants were divided into groups based on relative puberty speed. Those scoring less than 4 (the median point) were classified as early pubertal [n=11]. Those scoring 4 or higher were classified as late pubertal [n=40]. Chi squared tests reveal no significant relationship between puberty speed and pheromone detection. [AND1 $\chi^2 = .001$, df=1, p=.98; AND2 $\chi^2 = .90$, df=1, p=.34, EST $\chi^2 = .01$, df=1, p=.95]

Mann-Whitney U tests reveal no significant relationship between age at first shave and ability to detect any pheromone [AND1: Z=-.03, n=52, p=.98; AND2: Z=-.50, n=52, p=.62; EST: Z=-.52, n=52, p=.54].

5.8 Discussion

5.8.1 The effect of pubertal timing on pheromone detection.

Hypothesis 3 is not supported. Self-reported pubertal timing has no effect on ability to detect putative pheromones in this experiment. It may be the case that the behavioural differences in mating strategy related to puberty are sufficient to propel an early developing male towards optimal reproductive rate without the necessity of increasing attention to cues of reproductive condition.

5.8.2 The effect of dominance on pheromone detection.

The data presented here give support to a general hypothesis that social status will influence pheromone detection. Hypothesis 1, that subdominants will be more sensitive to EST as a signal of fertility, is not supported. Hypothesis 2 is supported in that subdominant males are shown to be

more likely not to detect EST. Inspection of figure 1 shows, however, that dominants are not more likely to be detectors. This suggests that it is the inability of subdominants to detect EST that may be driving this effect. It is possible that subdominants should be expected to be less discriminatory than dominants, since they have fewer chances to mate. This would imply that it is worth subdominants taking any mating opportunity they can, even if they risk making an error by mating with a non-fertile female, since the benefits of even a single fertile mating considerably outweigh the costs of a non-fertile mating. Dominant males, by contrast, are likely to have had more previous, fertile matings than the subdominants, so the expenditure of energy on further, non-fertile matings is maladaptive. This is similar to the error-management theory of between sex differences in human mating strategy as advanced by (Haselton & Buss 2000).

Complete explanations of this phenomenon are dependent on more complete knowledge of the informational content of the estratetraen signal. The results here are consistent with EST being an indicator of pregnancy. This conclusion would be strengthened if it could be demonstrated that dominant men show an aversion to estratetraen, since the hypothesis is contingent on them not mating with females on whom they detect the compound.

To further investigate this possibility, data from an earlier experiment was examined.

5.9 *Sample 2: Preferences for 1,3,5(10),16-estratetraen-3-ol (EST) and male-male competition.*

5.9.1 *Methods 2*

49 18-25 year old, heterosexual, Caucasian males were recruited during the summer of 2003.

Participants were presented with three examples of each pheromone. Pheromones were presented in groups of three, AND1, AND2 and EST. Pheromone presentation within each set was randomised. Each incidence of each pheromone was labeled differently and participants were not told that stimuli would be repeated. Participants were asked if they could smell anything in each bottle

before being asked to rate any odour detected, imagining that the odour was associated with a person, on attractiveness for a long-term relationship (on a 7 point Likert-type scale from 1(not at all attractive) to 7 (very attractive)). Therefore, only detectors for each pheromone were included in the sample. Each participant was tested twice, once in the morning and once in the afternoon, to control for potential diurnal shifts in hormone levels. The procedure resulted in 2 x 3 sets of results for each putative pheromone, which allowed a mean attraction rating to be calculated. Although the dominance inventory as administered in sample 1 was not included in this experiment, two other dominance measures were included. These were 7 point Likert-type scale responses all ranging from 1, not at all, to 7, very much, on: *how dominant to you consider yourself to be?* and *how competitive are you?* Since the questions in the dominance inventory may be strongly related to within-sex competition, either of these questions may be related to the construct.

5.9.2 Results 2.

Spearman's rank order correlations show no significant relationship between the general dominance variable and long-term attractiveness rating [AND1: $r=-.23$, $n=43$, $p=.14$; AND2: $r=-.28$, $n=49$, $p=.06$; EST: $r=-.21$, $n=46$, $p=.17$], although general dominance and attractiveness rating of AND2 show a negative trend. Competitiveness does not correlate with attractiveness rating for either male pheromone [AND1: $r=-.18$, $n=43$, $p=.25$; AND2: $r=-.21$, $n=49$, $p=.15$], but correlates negatively with attractiveness rating of the female pheromone [EST: $r=-.32$, $n=46$, $p=.03$] showing that males who self report as being more competitive are less attracted to the odour of EST (see figure 5-2).

5.10 General Discussion: dominance and pheromones in humans.

The difference between the assessment of dominance in the two experiments is an obvious weakness and, as such, conclusions remain largely speculative. There is sufficient evidence, however, to support a suggestion that dominant (high competitive) human males are not only more

sensitive to estratetraen but may also have an aversion to it, or are, at least, less attracted to it than subdominants (low competitive). If the assumption is made that EST is a pheromonal indicator of pregnancy, then this is in line with evidence from studies of other anthropoid primates showing that dominant males are less likely to attempt copulations with pregnant females (Engelhardt et al. 2007).

Anthropoid primates seem to have difficulty in assessing pregnancy in females. In chimpanzees, females have a customary 'slumped' posture that obscures their abdomen from view, making pregnancy difficult to visually assess, at least by human observers (Townsend, 2007, pers. comm). Pregnancy in humans may be more easily visually detected due to their upright posture which exposes their abdomen. If so, then this phenomenon may represent an anthropoid adaptation towards avoiding false-estrus that has become relict in humans.

Dominance has been associated with elevated glucocorticoid production in a variety of primate species (Creel 2001; Muller & Wrangham 2004a; Sapolsky 2005). In human males, self reported dominance has been shown to correlate positively with salivary cortisol (see Chapter 10).

Glucocorticoids have been shown to have an integral relationship to the development of olfactory receptors (Robinson et al. 1998), while medical treatment with cortisol has shown to have a beneficial effect on loss of sense of smell in humans (Heilmann et al. 2004). Cortisol may therefore be proposed as being integral to a potential mechanism by which sensitivity of dominant males to the odour of the putative female pheromone can be increased. The fact that cortisol can be used to increase olfactionary ability in clinical anosmics suggests that this effect may be plastic; that is that subdominant males may show an improvement in sense of smell as they increase in dominance and their cortisol levels accordingly increase.

5.11 Conclusion

The data presented here show a link between a social variable (i.e. dominance) and a physiological variable (i.e. ability to detect 1,3,5(10),16-estratetraen-3-ol), as part of a, presumably relict, anthropoid adaptation. The fact that no significant relationship is found between speed of puberty and any pheromone detection ability suggests that mating strategy changes made by life history trajectory may be found in the behavioural rather than the physiological arena. Also, the suggestion that the increased olfactory sensitivity of dominant males may be due to the action of cortisol on olfactory receptors and that this phenomenon may be plastic suggests that dominance may impact on mating strategy in non-permanent ways. By contrast, age of puberty cannot be altered once it has occurred and so may impact on mating strategy phenomena in more general, permanent ways. The findings here allow further predictions to be made on the effect of dominance on the ability to avoid non-fertile matings that are eminently testable in a wide variety of primate species.

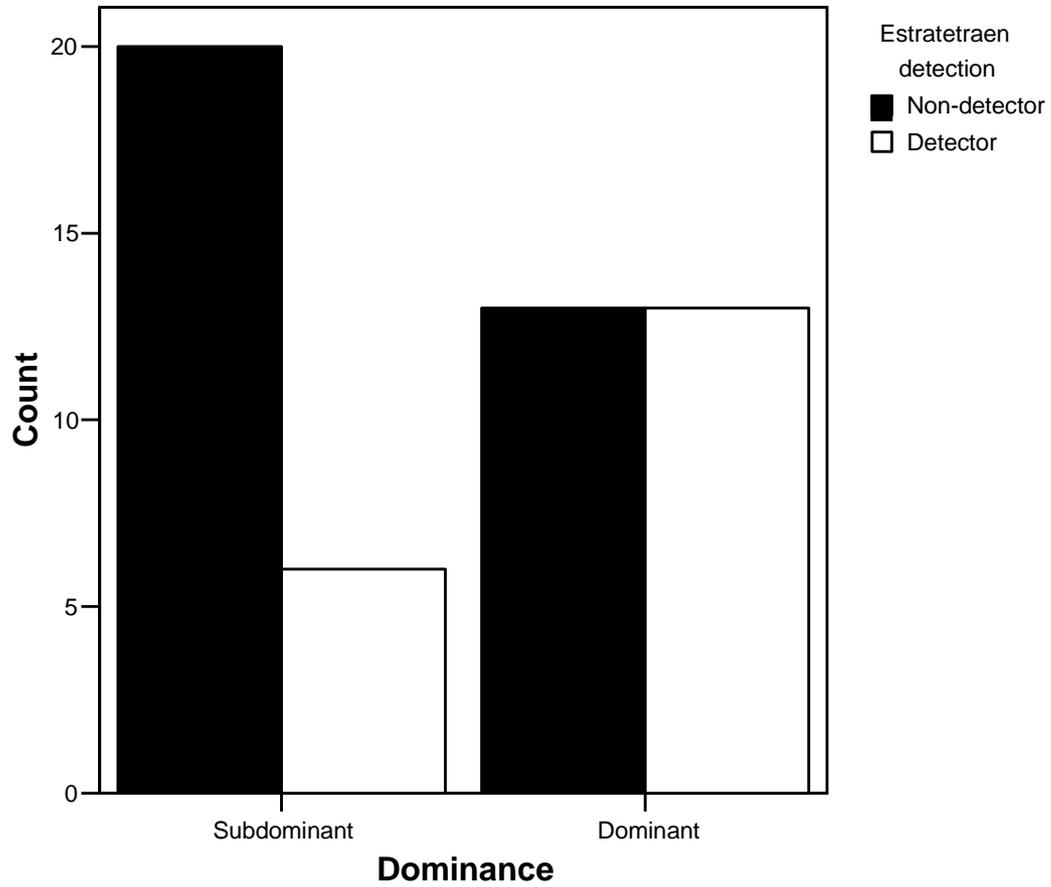


Figure 5-1: Subdominant males are significantly less likely to be detectors of the putative female pheromone 1,3,5(10),16-estratetraen-3-ol.

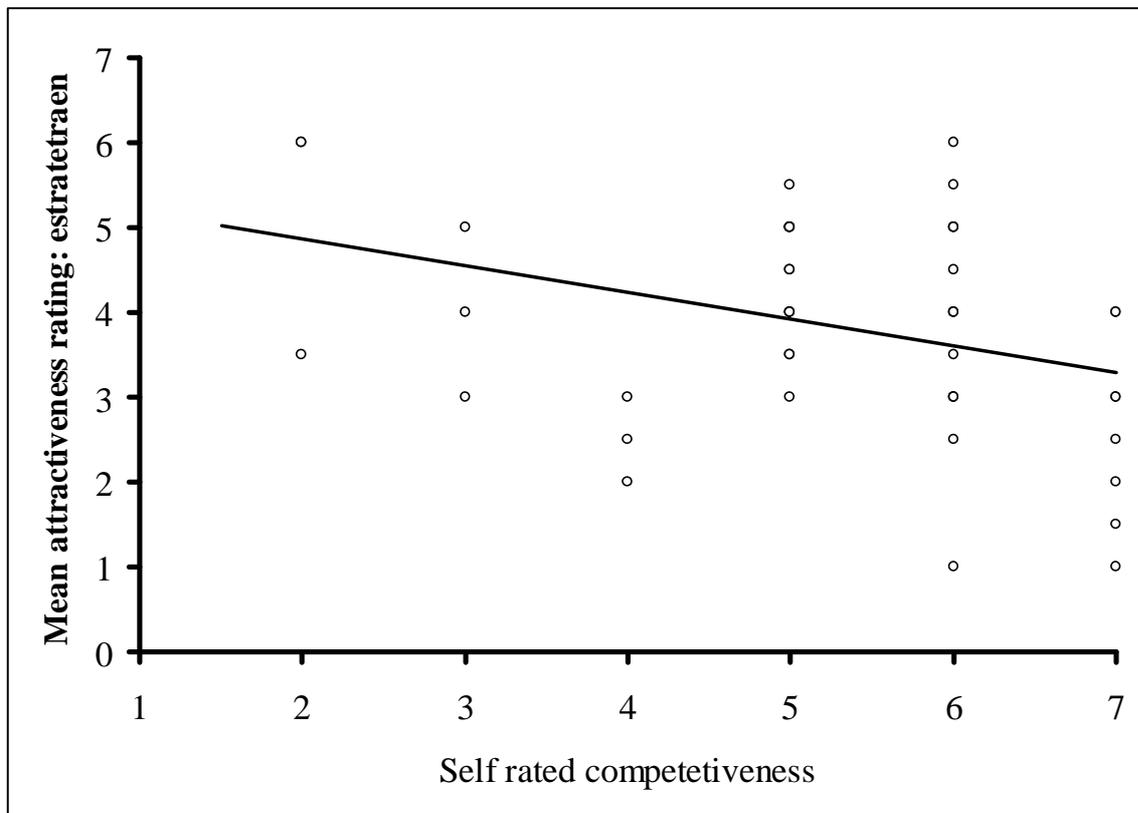


Figure 5-2: Males self-reporting as being highly competitive also report finding the odour of 1,3,5(10),16-estratetraen-3-ol less attractive.

6 Rated attractiveness, masculinity and apparent age relates to reported speed of puberty in adult males.

6.1 Abstract

Work on human life history suggests that human pubertal timing is linked to reproductive decisions. Early puberty is associated with a life history trajectory emphasising early and prolific reproduction. Kinsey et al. (1948), Belsky et al. (1991) and Ostovich & Sabini (2005) have shown that men reporting earlier puberty show enhanced male-typical behaviours such as aggression and greater interest in casual sex. Previous work has shown that men retrospectively reporting early puberty have higher levels of salivary testosterone. In a sample of 41 adult men, reported age of puberty and pubertal development relative to peers is shown to have a relationship with rated masculinity and attractiveness and also with apparent age.

6.2 Introduction

The age at individual humans go through puberty, as one of a number of life history markers, has been proposed as an adaptively plastic trait which can be adjusted to promote reproductive decisions that are optimal to a given environment (Chisholm 1993; Mace 2000; Stearns 1992; Stearns 1977) Such reproductive decisions are made in order to optimally allocate finite energetic, time and other resource budgets to a series of paired choices between, for example, current and future growth, current and future offspring and offspring quality versus offspring quantity. This produces two broad alternative life history trajectories for an individual organism; mature quickly,

begin reproduction early and produce a high number of lower quality offspring or mature slowly, delay first reproduction and produce a small number of higher quality offspring (Black & DeBlasie 1985). The allocation of effort to one path or the other is dependent on the environment in which the individual organism finds itself, and specifically in which it spends its early (childhood) years (Cornwell et al. 2006). Since the outcome of an appropriate life history decision is reproductive success, and increased fitness, evolutionary pressure should act to produce organisms capable of the optimal allocation of effort to one broad category of investment or the other (Chisholm, 1993; Stearns, 1992, see Chapter 1).

Late physical maturation is only optimal in an environment where resources are plentiful and chances of individual survival are high (Stearns 1992). Individuals developing in secure, stable environments should demonstrate behavioural and physical traits geared towards the production of a small number of high quality offspring, each of which represent a large and secure investment. Stressful environments, according to the same rationale, should promote early maturity and early first birth as part of a life history trajectory that places emphasis offspring quantity over offspring quality (Stearns, 1992, Chisholm, 1993). In humans, a secular trend towards earlier pubertal development has been shown among individuals of low socioeconomic status, lending support to these predictions in *Homo sapiens* (Mace, 2000), while early life stress has also been shown to accelerate puberty in girls (Belsky 1997; Belsky et al. 1991; Jones et al. 1972; Moffitt et al. 1992) in line with life history predictions.

If early developing males are placed on a life history trajectory emphasising early reproduction, they should demonstrate behavioural and physical characteristics in line with this trajectory. Kinsey et al., (1948) report that males reporting early puberty also report higher sexual drive, earlier loss of virginity and greater numbers of sexual partners than later developing males, while Ostovich & Sabini (2005) have shown that early maturing males report unrestricted sociosexuality (Gangestad

& Simpson 1990; Gangestad & Simpson 2000; Simpson & Gangestad 1991). Chapter 2 of this thesis also reports this relationship. Belsky et al. (1991) suggest that males going through puberty early (as a direct response to their life experiences in early childhood) also show exaggerated male-typical traits such as physical aggression. These behavioural traits may be linked to the action of testosterone on the behaviour of early developing males, who have been shown, in previous results, to have higher levels of salivary testosterone than later developers. The differing testosterone levels may also have an impact on the appearance of early-puberty males, since the sex hormone testosterone is responsible for most of the sexually dimorphic features that define the masculine facial 'look' (e.g. robust mandible, heavy brows, beard growth, (Thornhill & Gangestad 1999). Earlier developing males may therefore appear more masculine. Enhanced masculinity may also enhance the attractiveness of the individual males, although the relationship between masculinity and attractiveness in males is not necessarily positive in all circumstances (see Penton-Voak and Perrett, (2000) for review).

Males who go through puberty earlier are, by definition, developing faster than their peers. This may impact on their *biological age*, that is the difference between their actual age and the age which they appear to be. Males who are ageing 'well', will look younger than their real age and have a low (or negative) biological age. Males ageing 'poorly' look older than they are and have a high biological age. Males reaching physical maturity earlier than their peers will, before their later puberty counterparts also go through puberty, necessarily look older. Even after the slow developers have caught up, however, the early developers may maintain an older appearance.

From the above, the following hypotheses are advanced:

1. Adult men who have gone through puberty earlier will appear more masculine and more attractive.

2. Adult men who have gone through puberty earlier will look older than they are and have a higher biological age (= perceived - real age).

6.3 *Methods*

6.3.1 *Participants*

55 male, Caucasian participants, Mean age = 20.78 years SD=1.49, age range 18-25, were recruited from the undergraduate population of the University of St Andrews as part of a larger investigation into the relationship between sex hormones and puberty. Participants were also asked to give their consent to have their photographs taken and rated by 41 independent, anonymous raters for the current study. 41 of the original 55 gave full consent for this procedure.

6.3.2 *Questionnaire*

Participants were presented with a computer based questionnaire, which they answered in laboratory conditions. The questionnaire gathered demographic information (age, ethnicity, country of residence etc) and weight (kg) and height (cm) which were used to calculate Body Mass Index (BMI). Puberty speed was assessed with two items as presented in previous chapters; Age of Puberty: *At what age did you first shave?* (choice of age from 8 - 25 from a drop down menu) and Relative Puberty Speed: *Compared to your peers at the time, did you go through puberty much earlier/ much later* (on a Likert-type scale 1-7 where 1 = much earlier, 7 = much later).

6.3.3 *Photography*

Participants were seated in front of a neutral, standard grey background, 100 cm away from a Fujifilm Finepix S2 Pro camera, which was 135 cm from the floor, mounted on a tripod. Images

were recorded, uncompressed, at a resolution of 1200 x 1000 pixels with 24-bit RGB colour encoding, and were resized and cropped (see 'Rating faces' below) to a size of 348 x 527 pixels. Participants were asked to look directly at the camera and to keep their face relaxed and neutral.

6.3.4 Rating faces

Photographs were presented unmasked (i.e. containing some hair) but close cropped to remove as much of the grey background as possible while displaying all of the face. Stimuli were presented to the independent raters on a computer monitor and were rated for attributions of attractiveness and masculinity on 7 point Likert-type scales presented with each image (e.g. 1=very unattractive, 7=very attractive) and age in a free text entry field, limited from 1-99. 17 males and 24 females were recruited from the undergraduate population of St Andrews. Rater age ranged from 18 to 30 years, mean age = 21 years, SD=3.29. Inter-rater reliability was quite high for each attribution, with Cronbach's alpha scoring $>.9$ in each case. Mean attribution scores were calculated for each participant, using individual scores from all raters.

6.4 Results

Shapiro-Wilk tests showed that real age and both puberty variables were non-normally distributed ($p<.05$) so Spearman's Rank Order correlations were used to examine relationships between variables. One individual did not answer the relative puberty speed question, so the sample size drops to 40 for this variable.

Biological age was calculated by subtracting real age from rated age of each photographed participant. The mean biological age of the sample was 0, SD = .98, ranging from -1.97 (looking younger than their age) to 2.03 (looking older than they are).

Relative puberty speed correlated positively with rated masculinity [$r=.35$, $p=.029$] and with rated attractiveness [$r=.58$, $p<.0001$] (see fig. 6-1), indicating that men who report faster puberty than their peers are also rated as being more masculine and more attractive. Age of first shave also shows a negative relationship with these variables, although is not significant [rated masculinity: $r=-.23$, $p=.16$, rated attractiveness: $r=-.21$, $p=.20$]. Biological age correlates negatively with age at first shave [$r=-.334$, $p=.03$] (see fig. 6-2) and shows a similar trend with relative speed of puberty [$r=-.30$, $p=.06$], indicating that men reporting early development appear older than their counterparts.

6.5 *Discussion and Conclusions*

Hypothesis 1 is supported in that the faces of adult (i.e. post-pubertal) men who report earlier puberty are rated as being more masculine and more attractive than later developing men.

Hypothesis 2 is also supported, in that post-pubertal males reporting earlier pubertal development are rated as looking older than they actually are.

These findings are consistent with behavioural differences between fast and slow developing men as reported by Kinsey et al. (1948), Belsky et al. (1991) and Ostovich and Sabini (2005). Early developing men, as well as displaying more male-typical behaviours, also look more masculine facially. Their increased attractiveness is in line with an increased tendency to engage in a multiple-partner mating strategy, since high physical attractiveness would be necessary to attract multiple partners.

Figure 6-3 demonstrates the differences between slow and fast developers by comparing composite faces made from the 10 slowest and fastest developing respectively from this sample. The composites themselves were not rated, but mean results for the component participants are shown in the figure. The composite made from early developing participants appears to be more masculine, older looking and more attractive than its' counterpart.

Given that the early developing men in this sample appear more masculine *and* more attractive than later developers, they would be ideal men for women to target, as part of a female dual mating strategy, when at their most fertile (Penton-Voak et al. 1999). High masculinity and high attractiveness should indicate good immune system functionality (Penton-Voak et al., 1999). Since women have been shown to find masculine men attractive specifically for short-term, sexual encounters (one night stands), it would seem reasonable that men occupying this niche would have a complementary mating strategy and be more disposed than less attractive, less masculine looking men (the later developers in this sample) to show a preference for casual sex. This has been shown in Chapter 2 and also by the work of Ostovich and Sabini (2005). This means that the appearance of the early developing men may be driving their tendency to adopt a short term mating strategy. Nevertheless, the appearance and behaviour of early developing men in these samples are in line with predictions, drawn from life history theory, that place them on a rapid development trajectory with associated preferences for early and rapid reproduction.

If early developing males continue to look older for their age than later developers do across their lifetime, then this could represent a cost to the early development trajectory, assuming that looking older for one's years eventually decreases attractiveness. Evolutionarily this may not have been a serious setback, however, as the early development trajectory is theoretically an adaptation towards high-risk environments where mortality risks are high and individuals may have not lived long

enough for increased biological age to impact negatively on their attractiveness. This possibility forms the basis of the investigation in Chapter 11.

In general, these results suggest that life history decisions promoting speedy reproduction have effects not only on behaviour (Kinsey et al., 1942, Belsky et al. 1991, Ostovich and Sabini, 2005) but on appearance. One possible factor linking physiological to behavioural differences is the sex hormone testosterone. The relationship between testosterone and puberty is investigated in the following chapter.

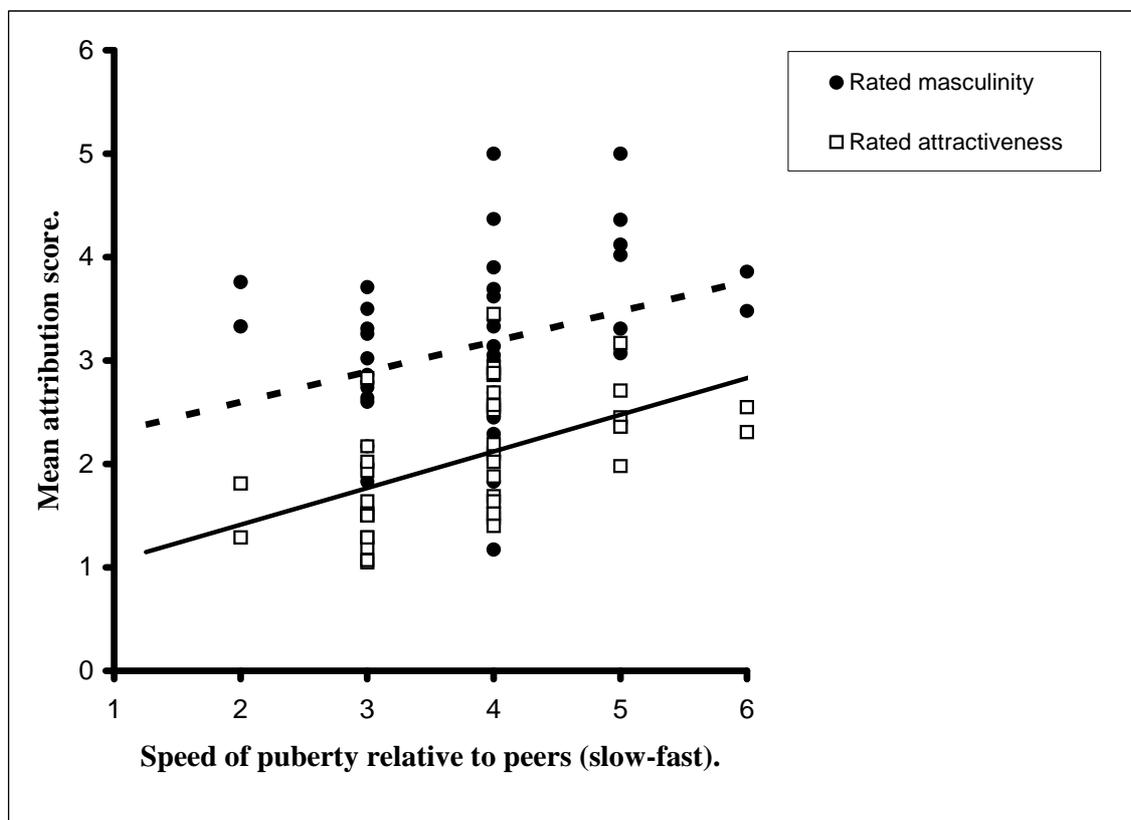


Figure 6-1: Positive relationship between speed of puberty (relative to peers) and both rated masculinity and attractiveness.

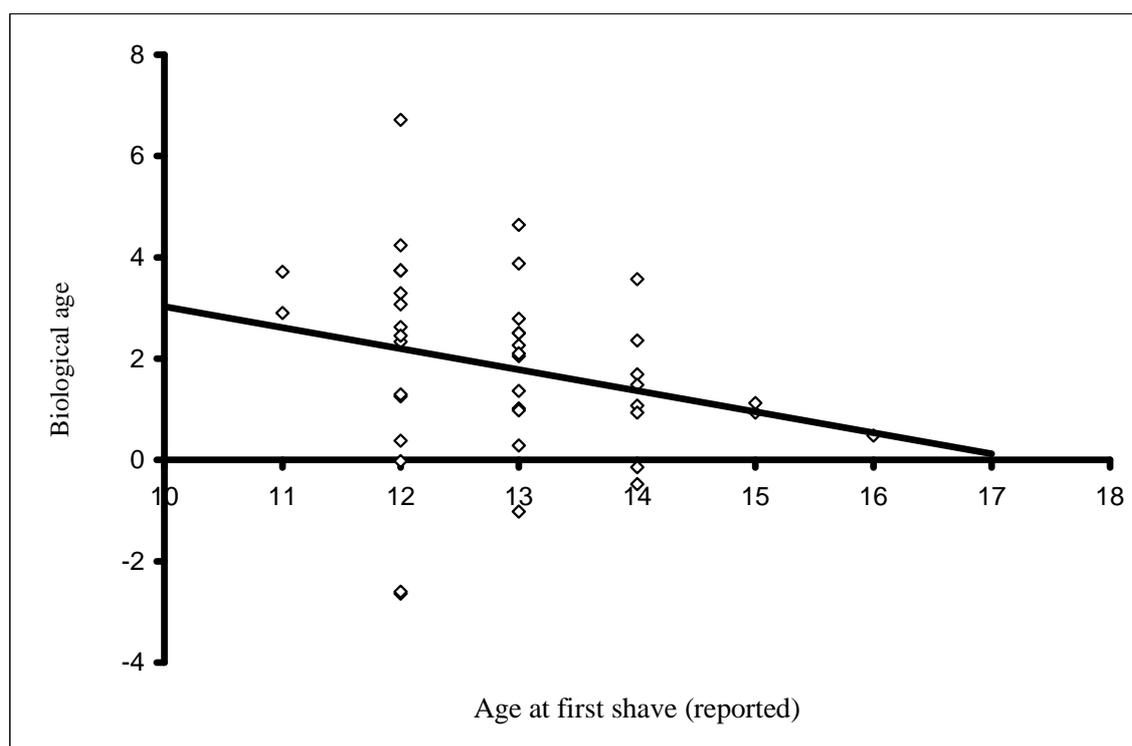
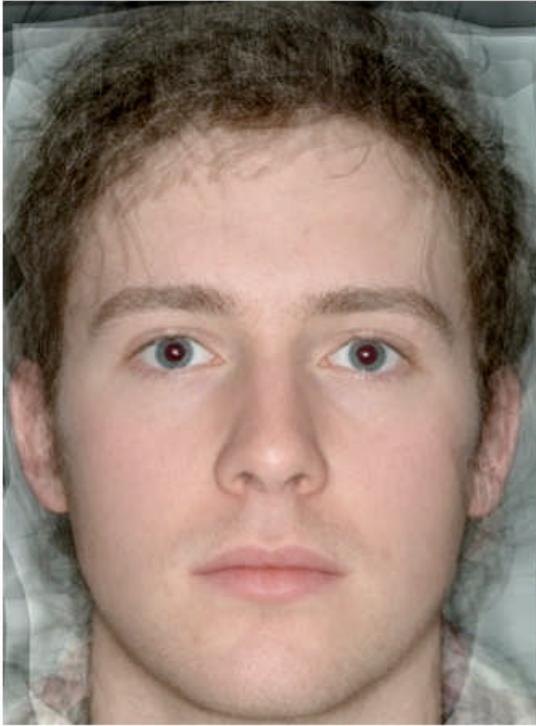


Figure 6-2: Negative relationship between reported age of first shave and biological (perceived – actual) age.



Age: 20.3 +/- .68 yrs
Age at first shave: 13.5 yrs
Slow puberty: 2.9
Rated Age: 22.6 yrs



Age: 20.6 +/- 1.17 yrs
Age at first shave: 12.1 yrs
Fast puberty: 5.2
Rated Age: 23.3 yrs

Figure 6-3: Composite faces made from ten slowest (left) and ten fastest (right) developing men.

7 Pubertal timing and salivary testosterone in men.

7.1 Abstract

Life history researchers have shown that the broad life history trajectory of an individual has wide-ranging effects on the timing of key reproductive events and on behaviours associated with them. Kinsey et al. (1948) and Belsky et al. (1991) and Chapter 2 of this thesis have shown that aspects of behaviour in adult (i.e. post pubertal) men can be predicted from their pubertal timing, while Chapter 6 shows that early puberty is associated with increased masculinity in male faces. As such, there should be an underlying physiological link between pubertal timing and behaviour. Since early developing males display a greater level of masculine behaviours than late developers, testosterone may be higher in early developing than in later developing men. In a sample of 48 adult males, post-pubertal salivary testosterone assays show that men reporting earlier pubertal development relative to their peers have higher mean testosterone levels as adults.

7.2 Introduction

This chapter investigates testosterone as a potential hormonal link between the increased masculine typical behaviours of early developing men (unrestricted sociosexuality; Kinsey et al., 1948; Belsky et al. 1991; Ostovich and Sabini 2005 this thesis Chapter 2), their more masculine facial appearance (Chapter 6) and the process of puberty itself (see Chapter 1).

7.2.1 Sex hormones and sex differentiated traits.

Androgenic and oestrogenic steroids are responsible for the sexual-dimorphism in human genitalia (Hughes et al. 2001), facial structure (Law Smith et al. 2006) and brain organization (Herman-

Jeglinska et al. 1997; Pol et al. 2006). As such, between-sex differences in sex hormone levels may be reflected in sex-typical behaviours. For example, men are reported as being more aggressive and more dominant than women (MacCoby & Jacklin 1980; Ramirez et al. 2001). Within sex differences in aggression and dominance have also been linked to individual variation in testosterone levels among adult men (Archer (1991), but see Albert et al., (1993), for alternative explanations). That is; that men with higher levels of circulating testosterone tend to be more aggressive and engage in dominance-enhancing behaviours as adults more often than low testosterone counterparts (Mazur & Booth 1998; Olweus et al. 1980; ZITMAN & NIESCHLAG 2001). It is interesting, given this, that Belsky (1991) also reports that males (but not females) set on the early development, Type 1 strategy are more prone to aggression than those on Type 2. Men are, on average, more interested in casual sex, have higher sex drives than women and generally report higher numbers of sexual partners (Gangestad and Simpson, 1991). It is likely that intrasexual variation in behaviour that is typically sexually dimorphic is in some part due to the organisational effect of testosterone on the brain.

Mikach and Bailey (1999) showed that women with a greater than average number of sexual partners consider themselves to be and were rated by experimenters as being more masculine. Although testosterone in their sample was not assayed, Mikach and Bailey's findings suggest that there is a link between several different aspects of male-typical behaviour that may be mediated by physiological, possibly hormonal events. As Mikach and Bailey suggest; "both unrestricted sociosexuality and masculine gender identity and role [may be] indicators of an underlying masculinization of the brain" (p149).

Testosterone in males has also been linked with relationship status, with partnered males (those in marital or long-term relationships) showing consistently lower testosterone than single men (Booth & Dabbs 1993; Burnham et al. 2003; Mazur & Michalek 1998) while *polyamorous* (maintaining committed relationships with multiple partners, as distinct from *polygynous*) males and females

both show higher testosterone levels than *monoamorous* or single individuals of the same sex (van Anders et al., in press). As such, it seems that the androgen testosterone has a key role to play in the mediation of mating strategy and in the implementation of sexual behaviour, at least with respect to partner numbers.

Puberty as a factor relating to both hormonal activity and sexual behaviour has received some attention, although has not been extensively investigated (see Ostovich and Sabini, 2005 for review). Kinsey et al. (1948) were the first to report an association between pubertal timing and sexual behaviour. According to Kinsey et al., adult men, but not adult women, retrospectively reporting early puberty showed higher sex drives and had more sexual partners (of both sexes) and a higher frequency of intercourse and orgasm than later developers, although Kinsey's conclusions were based on personal interviews rather than experiment. More recently, Ostovich and Sabini (2005), have shown empirically that men reporting early development score high on Gangestad and Simpson's Sociosexuality Orientation Inventory (SOI), indicating an unrestricted sociosexuality (characterised by higher numbers of sexual partners and one night stands) (Gangestad and Simpson, 1990, 1991 and 2000). Men score higher on the SOI than women on average, and high SOI score is associated with masculinity (Gangestad and Simpson, 1991).

Early developing human males, as adults, appear to be demonstrating more masculine-type sexual behaviour than later developing men, in terms of their sociosexual orientation. The aim of the current study is to investigate the relationship between progression through puberty and the male sex hormone testosterone, assayed in young adults aged 18-25. The hypothesis, based on the above, is that early developing males will have higher levels of circulating testosterone as adults than later developing males.

7.3 *Method*

7.3.1 *Participants*

55 Caucasian male participants were recruited from the undergraduate population of the University of St Andrews between February and March 2006. Mean age = 20.78 years SD=1.49, age range 18-25 years.

7.3.2 *Questionnaire*

Participants were presented with a computer based questionnaire on their first visit to the lab, which they answered in laboratory conditions. The questionnaire gathered demographic information (age, ethnicity, country of residence, etc.) and weight (kg) and height (cm) which were used to calculate Body Mass Index (BMI). Puberty speed was assessed with two items; Age of Puberty: At what age did you first shave? (choice of age from 8 - 25 years from a drop down menu) and Relative Puberty Speed: Compared to your peers at the time, did you go through puberty much earlier/ much later (on a Likert-type scale 1-7 where 1 = much earlier, 7 = much later).

7.3.3 *Hormone analysis.*

Participants were given polythene universal containers to deposit between 3 and 4 ml of saliva during the 5-10 minutes following arrival in the lab and experimental briefing on two separate occasions, each between 1400 and 1500 hrs and at least 24 hours apart. Participants were instructed to first rinse their mouths with water and then salivate passively into the containers rather than

chewing a wad of cotton wool to avoid possible inflation of the testosterone levels (Granger et al. 2004) or contamination with phytoestrogens. Participants had not eaten for at least an hour prior to testing sessions. Saliva was then frozen at -20°C until analysis. Hormonal data were assayed by the Biological Sciences Lab at Queen Margaret University (QMU) using an 'in-house' enzyme linked immunosorbant assay (ELISA, Al-Dujaili (2006) ; Sharp and Al-Dujaili (2004)). The assay procedure was based on the indirect, competitive binding technique with samples first extracted using di-ethyl ether (the protocol is described more fully in Welling et al. (in press..)). Mean testosterone values across the two testing sessions were calculated. Average testosterone for the whole sample = 257.31 pg/ml, $N=55$, $SD = 56.74$ pg/ml. This is within the normal range for the QMU lab.

7.4 Results

3 participants were excluded from analysis on the basis of their Body Mass Index being greater than 30 kg/m^2 ('obese' according to conventional BMI categories). This was to control for potential effects of obesity on either testosterone levels (Haffner et al. 1993) or puberty itself (Lee et al. 2007). A further 4 participants did not return to give a second saliva sample so no mean could be calculated. The total sample size was therefore 48. One further participant did not answer the relative timing of puberty question so the sample drops to 47 for this variable.

Shapiro-Wilk tests revealed that, of the three variables, mean testosterone, age at puberty and relative timing of puberty, only mean testosterone was normally distributed ($p>.05$). Consequently, Spearman's rank order correlations were used in the analysis.

Age of puberty shows a non-significant, negative relationship with mean testosterone: average [$r=-.26$, $N=48$, $p=.08$].

Relative Puberty Speed correlates negatively with average testosterone [$r=-.31$, $N=47$, $p=.03$] (see figure 1).

7.5 Discussion

The hypothesis that earlier developing males will demonstrate higher levels of testosterone is supported using relative pubertal speed but not age of first shave as a marker of pubertal timing, although age of first shave shows a trend that also supports the hypothesis. This fits with findings that men reporting earlier puberty also report more male-typical behaviours (Kinsey et al., 1948; Belsky et al., 1991, Ostovich and Sabini, 2005) and suggests a physiological aspect of this behavioural difference. To the extent that testosterone should be expected to associate with increased masculinity, this finding is consistent with the results reported in Chapter 6; that earlier developing men have more a masculine facial appearance .

The processes of puberty are not completely understood (Brook 1999). Although the physiological changes that take place and the cascade of hormonal activity that causes them have been well investigated, the ultimate trigger of puberty is unknown. Brook (1999) suggests that the initial surge of hormones that are diagnostic of the onset of puberty may, in themselves, be dependent on pre-pubertal sex hormones. In the absence of further information, particularly regarding the relationship between sex hormones and the triggering of puberty, there are no grounds to speculate on whether high pre-pubertal testosterone leads to early puberty or early puberty causes an elevation in testosterone levels, or even whether the two are causally linked. It is possible, for example, that the propensity to engage in masculine-type behaviours raises testosterone levels in early developing males, rather than increased testosterone leading to a tendency to behave in a masculine manner. The results here may suggest that behavioural and physical differences linked to pubertal timing so far by this thesis have a relationship with the effects and actions of the male sex hormone testosterone.

8 Second to fourth digit length ratio associated with early development in human males, but not in females.

8.1 Abstract

Second to fourth digit length ratio (2D:4D) is a sexually differentiated trait that has been associated with exposure to prenatal androgens. Low 2D:4D is a putative indicator of exposure to high levels of androgens *in utero* and has been related to a large number of masculine-type traits in adult humans and to the ontogenesis of sexuality. In a sample of 48 males and 42 females, low 2D:4D is correlated with early pubertal development relative to peers in males but not in females. This may be due to maternal stress elevating testosterone levels in the womb, and is a potential mechanism for the adjustment of life-history trajectories in response to stressors in the natal environment.

8.2 Introduction

Second to fourth digit length ratio (2D:4D) is a sexually differentiated trait (Manning et al. 1998b) with human males displaying consistently lower mean 2D:4D than human females across different cultural groups (Manning et al. 2002). The ratio is fixed by the 14th week of pregnancy (Manning et al., 1998) and is not affected by post-natal hormonal events such as puberty (Manning et al., 1998; Manning et al. 1998a; McIntyre et al. 2005). The ratio has been linked to prenatal exposure to testosterone and oestrogen *in utero*. 2D:4D appears to be negatively correlated with prenatal testosterone and positively with prenatal oestrogen (Manning et al. 1998b). Low 2D:4D has been associated with supposed masculine-type behaviours such as sporting ability (Manning & Taylor

2001), musical ability (Sluming & Manning 2000), psychoticism, neuroticism and sensation seeking scores (Austin et al. 2002) autism (Manning et al. 2001) and aggression (Bailey et al. 2005). Low 2D:4D has also been related to homosexuality in males (Lippa 2003; Rahman 2005; Robinson & Manning 2000) and masculine gender-role identity in women (Csatho et al. 2003). Although 2D:4D has been linked to many phenotypic correlates of testosterone, very little experimental work has taken place to support 2D:4D as an indicator of exposure to prenatal testosterone. A notable exception is the work of Romano et al. (2005) where experimental manipulation of yolk testosterone was shown to influence 2nd to 3rd digit length ratio in ring necked pheasants (for an account of avian digit homologies see Wagner and Gauthier, 1999), verifying that exposure to testosterone does affect digit formation. Further support for 2D:4D as a proxy for prenatal androgen exposure is found in the digit lengths of females suffering from Congenital Adrenal Hyperplasia (CAH). Females with CAH are exposed to unusually high levels of androgens *in utero* due to malfunctions in their adrenal glands (Berenbaum & Bailey 2003). Brown et al. (2002) show that females with this condition have lower 2D:4D than females without CAH, verifying the negative relationship between 2D:4D and prenatal sex-hormone exposure in humans, although a similar investigation conducted by Buck et al. (2003) fails to replicate this finding.

2D:4D has been associated with a number of other, sex-hormone linked traits. There is evidence that prenatal testosterone is involved in brain lateralisation with high levels of testosterone increasing the odds of left-handedness. Accordingly, Manning et al. (2000) find an association between low 2D:4D (the proposed 'high testosterone') condition and leftward asymmetry in speed of hand performance in children. Also, prenatal testosterone has been implicated in the aetiology of autism, with autistic children often showing increased levels of the male sex hormone (leading to the 'extreme male brain' theory of autism), while Manning et al. (2001) have shown that autistic children have significantly lower 2D:4D than the rest of the population. Low 2D:4D has also been

linked to increased fertility in terms of sperm counts in men, while high 2D:4D has been associated with low sperm counts and, in some cases, germ cell failure (Manning et al., 1998).

Prenatal hormones have an organising effect on the physiology of developing humans. Prenatal androgens are responsible for genital differentiation in males and females, and testosterone *in utero* is crucial to the normal development of the cardiovascular and central nervous systems in the male human foetus (Philips et al. 1994). Exposure to high levels of sex hormones during foetal development is theoretically responsible for the sexual differentiation of functional areas of the brain (Christiansen 2004; Herman-Jeglinska et al. 1997). Differences in behaviour as a result of this sexual differentiation of brain organisation require further activational hormonal events to make behavioural sex differences apparent. The hormonal cascade surrounding puberty is one such event (Christiansen 2004). Pre- and post-natal testosterone may therefore impact on differences in cognitive style and behaviours in post-pubertal male and female humans (Baron-Cohen 2002). Neither pre or post natal hormonal events alone are sufficient to induce behavioural change; an organisational difference requires activation in order to be expressed (Christiansen 2004). Between-individual variation in levels of hormone exposure *either* prenatally *or* peripubertally may therefore lead to individual differences in behaviour.

Individuals of many species, including humans (Mace, 2000), show accelerated development if placed under early life stress (Chisholm 1993; Reznick et al. 1990; Stearns 1992). This feature, according to life history theory, is an adaptation towards decreased longevity within a stressful environment, allowing an organism to begin reproduction early, produce more offspring and optimise inclusive fitness (Stearns 1992). Organisms should expect to share their environment with their mother, so evolution may have favoured individuals who can be primed to environmental conditions *in utero*. Human maternal stress has been shown to relate to gestation length (Dole et al. 2003; Wadwha et al. 1993) and to neonate birth size (Wadwha 2005) in ways which are consistent with life history theory which predicts a reduction in neonate size and inter-birth interval associated

with high stress environments (Chisholm 1993; Stearns 1992). Although these features are adaptive for the life history trajectory of the *mother* (unstable, stressful environments favour those who produce large numbers of low quality offspring with a low inter-birth interval (Stearns, 1992)), there is evidence that early birth in response to maternal stress can, in fact, be mediated by the foetus itself. Fetal-inflammatory syndrome is a multisystem stress response to maternal stress in the developing foetus that results in endocrinological changes in the womb which can trigger preterm birth (Wadhwa 2005). This improves the inclusive fitness of the foetal individual since high inter-birth interval of the mother implies more siblings and, therefore, a greater incidence of shared genes in the gene-pool. This may represent an adaptation of the foetus to the maternal environment, although this requires that pertinent information regarding the natal environment be available to the developing individual.

There are no direct neural or vascular links between the foetus and the mother, so there is no direct mechanism for the detection of maternal environment by the foetus. Furthermore, the developing foetus does not have a mature nervous system of its own (Wadhwa, 2005), so reception of and response to information regarding the natal environment must be mediated by another method. The placenta has been shown to be critical in mediating this relationship (Wadhwa, 2005). As well as acting as a transducer of critical maternal blood products, there is substantial evidence to suggest that the placenta acts as a sensory and effector organ for the foetus and that foetal responses to stress that would otherwise be mediated by the hypothalamic-pituitary-axis (HPA) are instead mediated by the placenta, since the HPA is unformed or immature. As an example given by Wadhwa (2005), the adult hypothalamus produces Corticotropin-releasing-hormone (CRH) in response to stress as a mechanism for controlling pituitary activity. In the foetus, identical CRH is produced by the placenta as a response to maternal cortisol, which is itself a response to stress.

Maternal stress has been shown to elevate uterine testosterone in rats (Herronkohl & Scott 1984) and testosterone has been positively correlated with stress in human females (King et al. 2005).

While the triggering mechanism of puberty in humans is unknown, prepubertal sex hormone levels are known to be important (Brook 1999). Among sheep, experimental manipulation of prenatal hormones has shown that increased exposure to androgens *in utero* leads to earlier pubertal development (Kosut et al., 2006). Exposure to higher levels of uterine testosterone, then, may be an indicator of maternal stress and, as such, may prime a developing foetus for early pubertal development.

With this in mind, we advance the following hypothesis:

As a marker of exposure to high levels of prenatal androgens, low 2D:4D will be associated with earlier puberty in humans.

8.3 Method

A sample of 48 men (mean age 20.0 years) and 42 women (mean age 20.8 years) was gathered from the undergraduate population of the University of St Andrews. Female participants were asked to report their age at menarche (first menstrual period), male participants were asked to report the age of their first shave. Because relative pubertal speed is likely to be more instructive than absolute pubertal age (which may vary between individuals due to socioeconomic differences) and because individuals may not be able to remember pubertal events accurately, participants were also asked to assess the speed of their pubertal development (“puberty speed” measure) relative to their peers (*Compared to my peers at the time, I went through puberty...*) using a 7 point scale where 1 is much slower and 7 much faster. After ensuring that the participant had not broken the index or ring finger of either hand, both hands of each participant were scanned using a Hewlett-Packard flatbed scanner. Digit lengths were measured from tiff images at actual size from the midpoint of the basal crease of the proximal phalanx to the most distal point on the finger using computer software. All data was coded and stored anonymously. Participants were paid for their involvement at the rate of £4 per hour.

8.4 Results

Mean 2D:4D was lower in the male participants than in the female participants [mean male = .963, $n=48$; mean female = .982, $n=42$; $t=1.62$, $n=90$, $p=.001$], showing the expected sexual difference in the trait. Shapiro-Wilk tests revealed that right hand 2D:4D and puberty speed are non-normally distributed [$p<.05$].

Spearman's Rank-Order correlations show that age at menarche/first shave did not correlate with 2D:4D in either sex [males: LH $r=.11$, $p=.45$, RH $r=.04$, $p=.78$, mean $r=.12$, $p=.42$; females: LH $r=-.12$, $p=.45$, RH $r=-.04$, $p=.81$, mean $r=-.05$, $p=.76$], although is in the predicted direction in males. Relative puberty speed did not correlate with 2D:4D in females [LH: $r=.15$, $p=.36$; RH: $r=.23$, $p=.14$; mean: $.17$, $p=.28$], but correlated negatively in males on average [$r=-.36$, $n=48$, $p=.01$, see fig. 8-1] and left hand 2D:4D [$r=-.34$, $n=48$, $p=.02$, see fig. 8-2]. This supports the hypothesis for males. Right hand 2D:4D shows a non-significant trend with puberty speed [$r=-.26$, $n=48$, $p=.07$, see fig. 8-3].

8.5 Discussion

In support of our hypothesis, we found that low 2D:4D was associated with faster reported pubertal development in men, but not women. If this effect is due to a rise in uterine testosterone associated with maternal stress, then this is potentially evidence for a mechanism by which maternal environmental stress can cause early development in male offspring as a foetal programming phenomenon. Testosterone itself may be counted as an environmental stressor for a developing foetus due to its immunosuppressant effects (Folstad & Karter 1992; Olsson et al. 2000; Thornhill & Gangestad 1999) which may lead to deleterious ontogenetic disturbances. As such, if early development is a result of prenatal exposure to high levels of testosterone, one might expect early developing individuals to show health problems later in life. While little relevant data has been

published, maternal stress has been identified as a causal factor of coronary heart disease, strokes, hypertension and diabetes in adults, potentially as side effects to prenatal adaptations to malnutrition (Barker 1994; Barker 2001; Roseboom et al. 2000), although there is no evidence that these effects are driven by testosterone. There are few conclusive results on the relationship between 2D:4D and adult health. Manning (2002) reports that high 2D:4D (low prenatal testosterone) is associated with elevated chances of myocardial infarction in men. This is counter to predictions, although testosterone is crucial to the formation of the male cardiovascular system *in utero* (Philips et al. 1994) so the relationship may be different from that with other health problems.

There are sources of uterine testosterone other than maternal metabolism. Leydig cells in foetal testes become mature around week 14 of gestation and begin producing testosterone at adult levels, continuing to do so for three months after birth (Rommerts 2004). If 2D:4D and speed of development are affected by foetal testosterone rather than maternal, then the case for testosterone as a mediator in the adjustment of developmental trajectory may be weakened; the association between low 2D:4D and early development may be due to individual variation in testosterone levels as a genetic, non-plastic trait, which is not altered by maternal condition. Leydig cells in adult male testes are stimulated in to testosterone production by the action of Luteinising Hormone produced by the pituitary gland (Rommerts 2004). Foetal leydig cells, however, produce testosterone as a result of the action of choriogonadotropin (hGC; structurally similar to LH) produced by the mother (Rommerts 2004). Furthermore, Ward et al. (2003) have shown that rat foetuses produce elevated levels of testosterone in response to maternal stress. Consequently, the foetus may produce testosterone as a result of maternal endocrine activity, and the link between maternal stress and uterine testosterone may be resilient. Nevertheless, conclusions remain speculative, especially given that there is no evidence here to suggest whether differences in developmental timing are being driven by trait or state testosterone; i.e. whether the mother's endocrinology has responded to environmental stressors during pregnancy, or whether the mother's testosterone levels are high in

general due, for example, to a psychosocial trait such as dominance (Grant 1994; Grant 1996; Grant 1998).

Manning et al. (2002 and 2003) have shown that 2D:4D is an indicator of androgen receptor variation. If variation in developmental effects of androgens are caused by the *sensitivity* of the individual to any quantity of hormones rather than by the amount of hormone to which they are exposed, then direct links to the maternal environment become less relevant. Instead, differences in pubertal timing may reflect the maintenance of an evolutionarily useful variation between males that allow at least some individuals to be well adapted, by chance, to environmental conditions.

The lack of significant correlation between ages of menarche or first shave and 2D:4D may reflect a lack of sensitivity of these variables as developmental markers in a mixed socioeconomic sample (in addition to the inability of men to recall accurately specific pubertal events, Kaiser and Gruzelier (1999), see Chapter 1). Variation in absolute age of puberty may be explained by differences in the environments in which the participants grew up. Age of puberty is affected by nutritional and socioeconomic factors (Palmert & Boepple 2001) which may vary between geographical areas and between sub-cultures. There is a reported difference in pubertal timing, for example, between town and country dwellers (Cameron et al. 1993) due, presumably, to differing conditions in the two environments. These effects may be bigger than the effects of uterine conditions on individuals *within* differing social and environmental groups. Participants drawn from an undergraduate population come from a wide variety of backgrounds and may display large individual variation in pubertal timing due to differences in socioeconomic environments in which they were raised. As such, it may be expected that the pubertal speed *relative to peers at the time* provides a more accurate indicator of variation since individuals may be more likely to have shared their early life environment with those peers.

The fact that this effect is not present in women is counter to predictions, since both sexes have an advantage in being able to adjust their life-history trajectories to suit environmental circumstances

and is, in this respect, evidence against exposure to prenatal testosterone acting as a mechanism for the adjustment of developmental speed. However, structural differences in anatomy between the sexes leads to differences in the amounts of testosterone produced and in sensitivity to testosterone. Men have more than three times the amount of testosterone than women, 95% of which is produced by the testes (Rommerts 2004). Male foetuses will therefore be exposed to larger quantities of testosterone than female foetuses once the Leydig cells become active at around week 14, the time at which 2D4D is set. Furthermore, male foetuses may be more sensitive to testosterone than female (i.e. have more androgen receptors) since androgens are crucial to male neural and cardiovascular development (Brinkmann 2001). Testosterone, then, may simply not be available to a female foetus in sufficient quantity for use as a signal of maternal environment, while the female foetus itself may not be sufficiently sensitive to it. Human females loose little from this, since the penalties of too early maturity for a female are potentially catastrophic (e.g. gestating a child before the pelvic girdle has completed growth could lead to the death of both mother and infant) while males face no such cost. Early development becomes maladaptive for human females much earlier than it does for human males. Using early, postnatal experience to modulate developmental trajectory may be a better strategy for a human female. Jeha et al. (2006) report a case of extreme precocious puberty (with pubertal development occurring around 2-4 years) in the males of one family, linked to a specific genetic mutation in their luteinising hormone (LH) receptors, which presumably promotes Leydig cell activity in the absence of appropriate hormonal signals. Interestingly, although some females of the family shared the mutant allele, they did not demonstrate precocious puberty. This may imply that the timing of puberty in males is closely linked to Leydig cell activity. Since Leydig cells are active and responsive to maternal hormones in utero, foetal programming of developmental speed is likely to be linked to the development of these features.

Having elder brothers appears to raise the amount of androgens to which a developing foetus is exposed (Williams et al. 1999). Since males face higher reproductive variance than females (a male

who is unsuccessful in the reproductive arena will do very much worse than a male who is successful), competition between males is extremely high. Thus, a male born into an environment in which there are already males present would have an advantage in developing faster (and perhaps developing a more masculine phenotype) in order to compete, even if the males with whom he is competing are his brothers. Females would not need a competitive advantage over older brothers, so there is no reason to predict a similar, fraternal effect on developmental speed in females. A similar rationale may predict that females with older *sisters* would need a competitive advantage, although female reproductive variance is comparatively low, and that females being born into an environment in which there are other, older females may be set on a different developmental and phenotypic trajectory in order to compete. The negative (although non-significant) relationship reported here between 2D:4D and pubertal timing in females is an intriguing result, since high 2D:4D is a marker for high oestrogen as well as low testosterone (Manning et al. 1998b). Any further speculation is unwarranted, however, in the absence of further results, particularly linking multiple female births to elevation of uterine oestrogen.

It is, finally, possible that males developing in a high testosterone environment may appear more masculine as adults and be more attractive (at least as short-term, reproductive partners, Penton-Voak et al., (1999)). As such, they may be able to optimise their inclusive fitness by reproducing early with multiple partners (the 'male-typical' reproductive strategy, Gangestad and Simpson, 2000). A male developing with lower levels of testosterone may be less masculine, and less physically attractive as a reproductive partner, so may be better served by delaying physical maturation in favour of continuing a period of social learning, in order to increase his potential as a resource-provider.

8.6 *Conclusion*

Low 2D:4D ratio (a putative index of prenatal exposure or sensitivity to androgens) is associated in the current sample with early pubertal development relative to peers in human males, but not females. This is potentially evidence for a mechanism by which the developmental speed of boys is adjusted to suit local environmental (perhaps demographic) conditions in response to maternal stress during pregnancy.

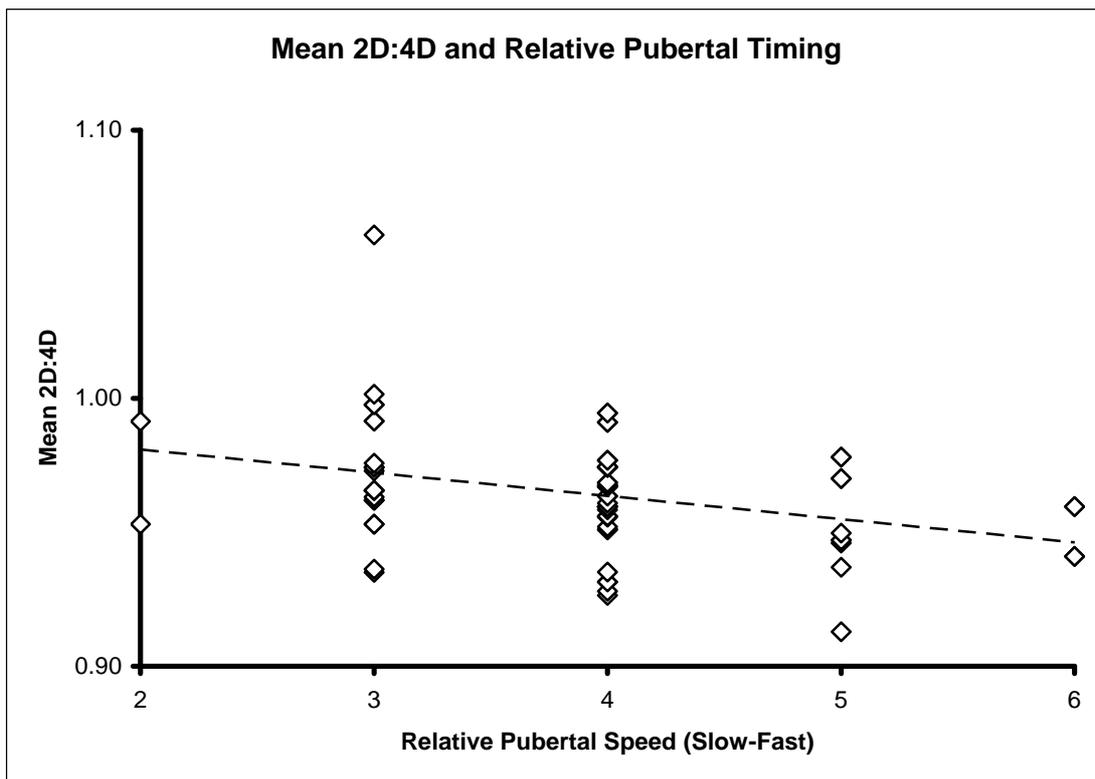


Figure 8-1: Mean 2d:4D correlates negatively with relative pubertal speed in males

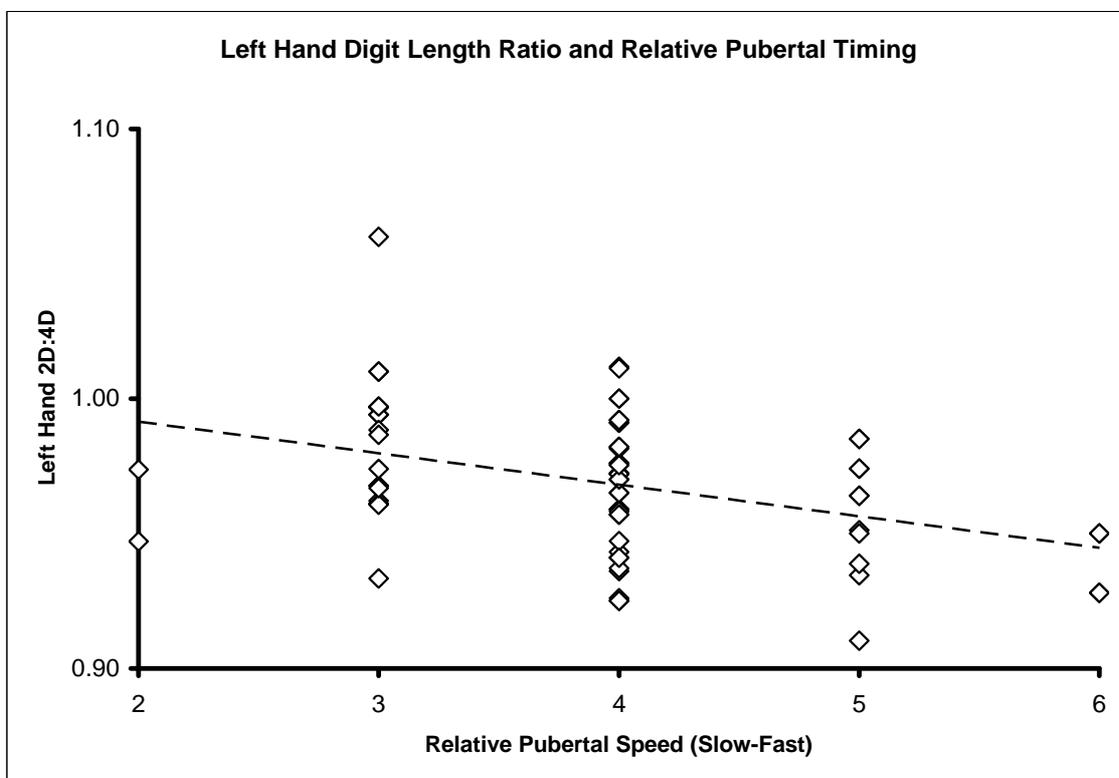


Figure 8-2: Left hand 2d:4D correlates negatively with relative pubertal speed in males

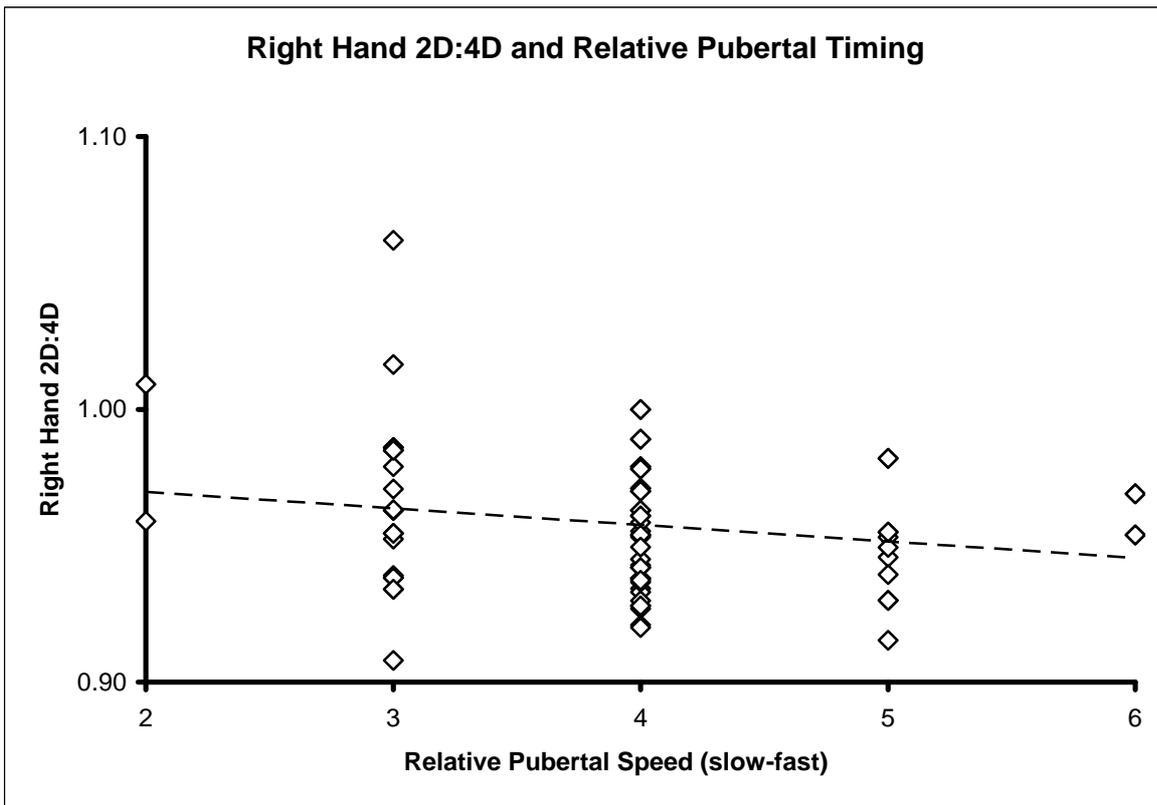


Figure 8-3: Right hand 2d:4D has a non-significant negative trend with relative pubertal speed in males.

9 Dominance and attractiveness: are dominant men attractive men?

9.1 Abstract

High dominance men should be attractive by dint of their increased mate-value stemming from their ability to control resources. Given that dominance should have a physical as well as social component, dominant men may also be more physically attractive than subdominant men. This is consistent with literature suggesting that attractive men are more influential and successful in the social or economic arenas. This hypothesis is investigated in two samples from previous experiments, one using self-rated attractiveness variables and one using independently rated facial attractiveness. In neither case does dominance appear to be associated with facial attractiveness, although men in the first sample consider their bodily, vocal and general attractiveness to be higher than subdominant men. Findings are thus consistent with ideas that high physical dominance increases attractiveness in that athletic fitness, masculinity and muscularity are important to both physical dominance and male attractiveness.

9.2 Introduction

Literature reviewed has suggested that dominant men should be more attractive owing to their high mate value which stems from their ability to control resources and influence the social arena (Hawley, 1999; Mueller and Mazur, 1998, Pawlowski and Dunbar, 1999 see Chapter 1). Human dominance, however, has a physical component and stronger men should be expected to be higher in dominance owing to their ability to intimidate and coerce others using their strength through

agonistic or aggressive acts (Hawley, 1999). As such, there is reason to suppose that high dominance men may have a distinct appearance from subdominant men. Given that attractive individuals have been shown to be more successful in various social arenas (job applications accompanied by an attractive photograph have been shown to be more successful, for example (at least when the quality of the resume is mediocre, (Watkins & Johnston, 2000)) and at trust-based economic games (Mulford et al. 1998; Zebrowitz et al. 1996), and that the halo effect of attractiveness should increase social influence, we should expect high dominance men to be more attractive.

Increased attractiveness may be either a cause or a correlate of increased dominance. Either way, the following prediction is advanced: high dominance will be associated with increased attractiveness in adult men.

9.3 *Sample 1: Self-rated Attractiveness*

9.3.1 *Methods 1*

The large, internet based sample from Chapters 2 and 3 was used, restricted to UK national, Caucasian men aged between 18 and 40 [mean age = 27.86, SD =6.47, n=3,846]. Responses to the social and physical (*Socially/Physically I am mostly...* on a 7 point scale from 1 (*submissive*) to 7 (*dominant*)) dominance questions were factored together to produce a single dominance measure. A single factor was produced, accounting for 71.90% of the total variance. Social and physical dominance both loaded on this factor positively at $r=.85$.

Participants were asked to assess their own attractiveness in a variety of different domains, each on a Likert-type scale from 1 (*extremely unattractive*) to 7 (*extremely attractive*); facial attractiveness (*My face is...*), body attractiveness (*My body is...*); vocal attractiveness (*My voice is...*) and general attractiveness (*In general I am...*).

9.4 Results 1

All variables (including age) violate a Shapiro-Wilk test for normality at $p < .0001$ and were rank transformed prior to regression analysis.

The four, rank-transformed self-rated attractiveness variables and age were entered in to a multiple linear regression (enter method) with self rated dominance as the dependent variable. A single significant model was produced [$F=178.71$, $df=5$, $p < .0001$]. General attractiveness [$\beta=.110$, $p < .0001$], vocal attractiveness [$\beta=.18$, $p < .0001$], body attractiveness [$\beta=.22$, $p < .0001$] and age [$\beta=.05$, $p=.001$] make unique, significant contributions to the model, although facial attractiveness does not [$\beta=.04$, $p=.10$]. Of all variables, body attractiveness contributes most to self assessment of dominance. This provides limited support for the hypothesis.

9.5 Sample 2: Facial Attractiveness (other rated)

9.5.1 Methods 2

Facial photographs of the same sample of 42 men introduced in Chapter 5 were rated by 41 independent raters, under identical conditions reported in that chapter, for physical attractiveness. The men were asked to report their dominance by reporting their own assessment of their social and physical dominance by responding to questions as presented in Chapter 2, and also by completing the dominance scale inventory, introduced in Chapter 7. Social and physical dominance items were combined in to a single score using factor analysis, producing a single factor which accounts for 53.65% of the variance. Both social and physical dominance measures load on this factor at .73. Mean dominance inventory score was 30.61, ranging from 7.86 (submissive) to 44.29 (dominant), $SD=7.10$.

9.5.2 Results 2

Shapiro Wilk tests reveal that the dominance scale results are non-normally distributed ($p=.01$), but both rated attractiveness [$p=.42$] and the dominance factor score [$p=.22$] are both normal.

Dominance scale was rank transformed before further analysis took place.

Pearson's product moment correlations reveal that neither self-rated dominance factor [$r=.02$, $p=.90$] nor dominance scale [$r=.16$, $p=.32$] score correlate with rated attractiveness. The hypothesis is not supported.

9.6 Discussion

Given that the independent ratings of attractiveness are made on facial photographs of men, the two samples converge on the conclusion that facial attractiveness is not linked to self-perceptions of dominance, counter to predictions. However, other aspects of male attractiveness do appear to be linked to men's assessment of their own dominance. Given that dominance should be expected to have a physical component, related to a man's ability to engage in physically aggressive or intimidating acts, it is not surprising that bodily attractiveness should relate to dominance, given that characteristics of the human male body that are attractive (e.g. broad shoulders, narrow waist, toned muscles (Fan et al. 2005; Horvath 1981; Singh 1995)) are to the most part related to athletic fitness and physical strength (Fan et al. 2005; Singh 1995). The fact that these features relate to both attractiveness (or at least to a man's own assessment of his attractiveness) as well as perceptions of his own dominance may be coincidental, owing to the fact that the ability to physically intimidate others and the attractiveness of the male body depend on a degree of physical, athletic fitness.

Feinberg et al. (2006) and Puts et al. (2006) have both shown that the human voice contains cues to

dominance, perceived masculinity and size and that these cues are related to the attractiveness of the voice to others, which is consistent with the finding here that men who consider their voices to be attractive also consider themselves to be dominant. The positive relationship between general attractiveness and dominance may involve both assessments of vocal and bodily attractiveness as well as a general assessment of own mate-value, which may, although this is speculative, involve consideration of personality traits and (potential for) resource control.

9.7 Conclusion

The data presented here suggest that, while facial attractiveness is not related to dominance in men, components of attractiveness that may relate to male-male competition (such as muscularity or athletic fitness) or other aspects of mate-value (such as wealth and status) may also, have a relationship with dominance. . Confirmation that bodily or vocal attractiveness is related to dominance would come from independent ratings of these traits in further experiments.

10 A cost of high dominance? Dominance and cortisol in men.

10.1 Abstract

Glucocorticoids are a diagnostic feature of stress. Recent work has shown that high dominance animals, particularly some primates, can be highly stressed, which was counter to predictions that loss of social control (i.e. subordination) would be stressful. Salivary cortisol is assayed in 52 men and is shown to correlate positively with self-reported dominance. Since prolonged exposure to cortisol puts humans at risk of health problems, this finding has implications for the links between social position and health.

10.2 Introduction

The release of glucocorticoids (in humans and primates cortisol and hydrocortisol) is a diagnostic feature of stress (Creel 2001). Glucocorticoids accelerate metabolic rate and minimise energy storage, priming the metabolism for a period of enhanced energetic store processing in preparation for a stressful event. This process is adaptive for short-term stressors, but prolonged exposure to endogenous glucocorticoids has deleterious effects on the health of an individual animal ((Creel 2001; Muller & Wrangham 2004b).

Animals placed in stressful situations show increased levels of glucocorticoid release if they have no control over their surroundings (Creel 2001; Muller & Wrangham 2004b; Sapolsky 2005; Weiss 1970). Rats respond to electric shock stresses less severely if they are given access to a lever that can stop the shocks or are given audible or visual warnings before shocks are administered (Weiss 1970). This leads researchers to assume that, in dominance hierarchies, subdominant animals would

be more acutely stressed than dominant animals owing to harassment from dominants and the lack of social control and influence they possessed (Creel 2001; Muller & Wrangham 2004b; Sapolsky 2005). Experimental evidence showed that physical fights between individual animals promoted a much larger increase in cortisol in losers than in winners, with losers of such encounters generally being termed 'subordinate' (Louch & Higginbotham 1967; Manogue 1975). Since prolonged cortisol exposure has catastrophic effects on fertility (Sanders & Bruce 1997), the maintenance of a stressed-state in subordinate animals was proposed as a mechanism for the suppression of breeding in subordinates by dominants (Brown 1978).

In a number of animal species, however, the reverse is true and dominance rank positively correlates with glucocorticoid production (Creel 2001; Creel et al. 1997; Muller & Wrangham 2004b; Sapolsky 2005). This may be due to the increased metabolic demands of high dominance caused by physical displays and aggressive encounters which are necessary to maintain high social rank (Muller & Wrangham 2004b). The degree to which subordination or dominance is stressful varies according to numerous factors related to the social organisation of the species under consideration, including dominance hierarchy style, mating strategy and resource distribution (Sapolsky 2005). In all cases, however, stress as a result of dominance has negative consequences to individual health, presumably through the action of glucocorticoids (Sapolsky 2005).

In many primate species, glucocorticoid production has been positively correlated with dominance rank (Sapolsky 2005). Here, we investigate the relationship between salivary cortisol and self-reported dominance in humans.

10.3 Method

52 men [mean age 20.8 years, SE .20, range from 18-25 years] were recruited from the University of St Andrews. Participants were given polythene universal containers to deposit between 3 and 4 ml of saliva during the 5-10 minutes following arrival in the lab and experimental briefing. Males

did this on two separate occasions, each between 1400 and 1500 hrs and at least 24 hours apart. Cortisol was assayed at Queen Mary University, Edinburgh, using an in-house ELISA, using the same protocol as reported for testosterone analysis in Chapter 7 (Sharp & Al-Dujaili 2004; Zitman & Nieschlag 2001). Cortisol was calculated as an average of the two samples provided by each participant. On their first visit to the lab, participants completed an 11 item dominance questionnaire from the International Personality Item Pool (as used in Chapters 7 and 9).

10.4 Results

Mean cortisol ranged from 1.82 pg/ml to 16.00 pg/ml with a mean of 6.43 pg/ml [SE=.49] in males. This is within normal range for the Queen Mary lab. Dominance score correlates positively with mean salivary cortisol in men [$r=.289$, $n=52$, $p=.04$]. See figure10-1.

10.5 Discussion and Conclusion.

Human male dominance is shown to associate with increased salivary cortisol. This has immediate implications for understanding the link between human social position and health. The dominance scale used here is distinct from an index of socioeconomic status and is, rather, a measure of social control and influence within an individual's own peer group. High dominance men are producing more stress hormones than subordinates, suggesting that in human males, popularity and influence have a cost. The cause of this stress is unknown, although it is possible that, despite of overt aggressive challenges to dominance being rare among humans, maintaining social networks is an energetically costly activity, perhaps due to the requirements of negotiation with and manipulation of a group of humans in order to retain high levels of influence and dominance, which may be analogous to the aerobic effort dominant chimpanzees invest in physical displays (Sapolsky 2005). These findings are consistent with the work of Creel (2001), Creel et al. (1997) Muller & Wrangham (2004b) and Sapolsky (2005) in that humans considering themselves to be high in dominance appear to be experiencing greater levels of stress. Sapolsky (1999) has suggested that

whether or not being at the top of a hierarchy is stressful is dependent on the stability of the social hierarchy at the time. An unstable or shifting dominance hierarchy is likely to lead dominant individuals to experience more stress, while a stable hierarchy should produce a low stress environment for high ranking individuals. After a recent transition of dominance, for example, an individual recently achieving high rank may have to fight to maintain that rank, experiencing an increase in stress as a result of increased effort. By contrast, an individual who has occupied high rank for some time, in a group where challenges to dominants are rare, would experience very little stress (Sapolsky, 1999; 2005). Within this context, the finding presented here suggests that human social organisation may be considered unstable, with high dominance individuals having to expend effort to maintain their status. It should be remembered, though, that the sample consists of young university undergraduates, who may be experiencing a less stable social hierarchy than is common to human society at large.

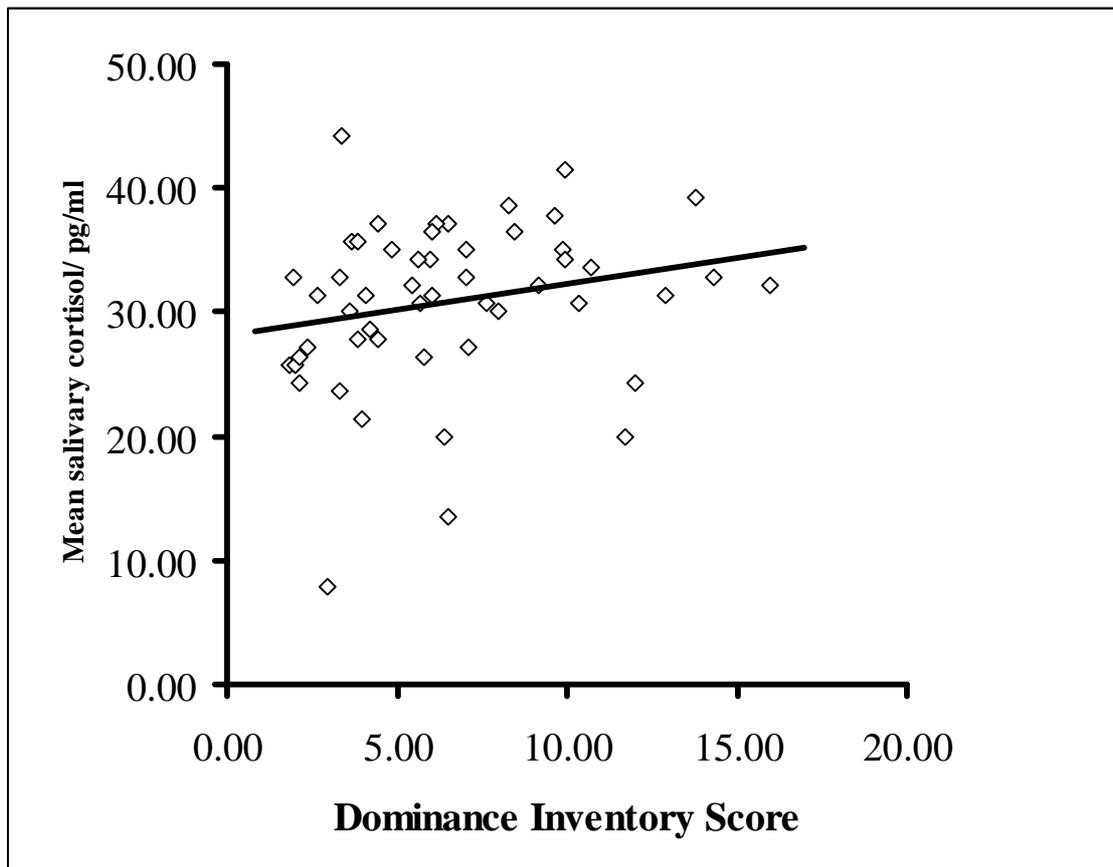


Figure 10-1: *The relationship between dominance inventory score and mean salivary cortisol in men.*

11 The cost of early puberty: skin phenotype, pubertal timing, testosterone and appearance.

11.1 Abstract

Previous chapters have shown that men reporting earlier puberty have higher salivary testosterone, a more masculine digit ratio, and have a more masculine and attractive facial appearance. Their faces also appear older than the late developers in their cohort. The central premise of life history theory is that organisms trade finite resources between investment in reproduction or the maintenance of body tissue. This thesis has so far assumed that phenotypic differences shown by early developing men are indicative of their investment in early reproduction over tissue maintenance. Skin ageing is a cellular process, consequently early developing males should show features in their skin associated with increased age. Furthermore, testosterone may inhibit the immune system and prevent the early developing men from protecting their skin adequately against environmental assault, so early developing men may show poorer skin quality than later developing men. Skin patches were extracted from facial photographs of 42 men. Texture was quantified using a Gabor wavelet analysis. Relationships were found between skin texture variables and pubertal timing, as well as between skin luminance and pubertal timing, while salivary testosterone correlates negatively with the mottled pigmentation and roughness of the skin. However, upon controlling for absolute variation in ambient luminance, many of the relationships disappear. Skin patch luminance remains a reliable correlate of pubertal timing, with early puberty being associated with darker, less reflective skin. Results are discussed with reference to human sebaceous gland activity.

11.2 Introduction

Men reporting earlier puberty relative to their peers have been shown to have higher salivary testosterone (Chapter 8) and more masculine 2D:4D (chapter 9.1), indicative of a greater exposure to prenatal testosterone, than men reporting later puberty. Furthermore, early developing men have been shown to have more masculine facial appearance (presumably due to the action of testosterone on facial bone structure) and to appear more attractive and older looking than their same-age, later developing peers (Chapter 7). These differences are consistent with the theory that early puberty in men is associated with a rapid life history trajectory.

A rapid life history trajectory is associated with decreased longevity (Chisholm, 1993; Stearns, 1977). This decrease has two sources; not only is the trajectory itself an adaptation towards an environment where long-term survival is not guaranteed and mortality risk is high (Chisholm 1993; Gasser et al. 2000; Stearns 1992; Stearns 1977), but investing time and energy in reproduction at the expense of growth, according to the central concepts of life history theory, *ipso facto* leads to earlier mortality (Lycett et al. 2000; Rhine et al. 2000; Stearns 1992). Individuals on a rapid life history trajectory are by definition developing faster than their slow trajectory counterparts (Stearns 1992). This difference is apparent in the sample in Chapter 7, where faster developing males are shown to be rated as looking older than their peers. This 'poor' ageing (looking older than chronological age) may be considered a cost of early development, and may project further in to adult life, with earlier developing men consistently appearing to be more advanced in age than the rest of their cohort across their life.

Among the age group presented in the previous chapters, appearing older than peers may not carry a particularly high cost, since there may be social and sexual benefits to looking older for young men.

Looking older than chronological age in middle age or in later life may have a more detrimental effect to attractiveness (Deutsch et al. 1986) and, hence, success in the social or mating arenas. This may be considered a long-term cost of accelerated development. Furthermore, if the difference between apparent and chronological age represents a real, physical difference in the biological age of an organism, because that organism is developing (i.e. advancing through its' life course) more rapidly, then appearing older may have a real cost to longevity. If this is the case, then rapid development, here indexed by early puberty, should have consequences to physiological ageing of an individual. While the increased apparent age of the early developing men in this thesis may be due to their increased masculinity of bone structure, leading them to appear more mature than their counterparts, their accelerated developmental trajectory may impact on other aspects of their physiology which may be literally older, at a cellular level, than their slower developing peers.

Cells steadily lose their replicative ability as they age, a phenomenon called cellular senescence (Jenkins 2002). This leads to morphological change and/or loss of function in most organs of the body and to most major physiological aspects of *intrinsic ageing* (i.e. properties of ageing that are due to internal aspects of physiology rather than to external, environmental factors, as opposed to *extrinsic ageing*). Human skin cells show cellular senescence, as indicated by a steady deterioration in tissue function across a lifetime, similar to that of most internal organs (Campisi 1998; Jenkins 2002). Differences in developmental trajectory that impact on physiological ageing may, therefore, be visible in the skin.

Skin texture has been shown to be important to both male and female human facial attractiveness (Fink et al. 2001; Jones et al. 2004a; Jones et al. 2004b) and specifically to carry information on individual health (Jones et al. 2004a; Jones et al. 2004b). Consequently any detrimental effect on skin texture associated with early development could be a genuine cost to attractiveness, at least later in life.

11.2.1 The Structure of Human Skin

Mammalian skin has three distinct layers; the hypodermis (or basement membrane), the dermis and the epidermis, each with a distinct structure and function. The dermis contains a large number of nerve endings, providing the sense of touch across the surface of the skin. The dermis also contains hair follicles, apocrine, sebaceous and sweat glands as well as the blood vessels which supply blood to the dermis and the lowermost cells of the epidermis. The dermis is primarily connective tissue which provides cushioning against stress for the body. The epidermis, the top layer of skin, is made up of a number of different types of cell. Most numerous, making up around 90% of total epidermal cells, are the keratinocytes which provide a keratinised, waterproof layer on top of the epidermis which protects against infection and invasion by pathogens. The other epidermal cells are melanocytes, which produce the pigment melanin, Langerhans cells, which are part of the skin's immune system, and fibroblasts, which are responsible for maintaining the extra-cellular collagenic matrix of all animal tissues. The epidermis contains no blood vessels of its own. Cells receive nutrients and waste removal via osmosis from dermal capillaries at the base of the epidermis before migrating towards the epidermal surface, steadily deteriorating and changing phenotype as they move further from the source of blood until they die on the skin's surface and are sloughed off (Carlson 2004).

11.2.2 Skin Ageing

There are two major influences to cellular ageing of the skin; extrinsic and intrinsic ageing (Jenkins 2002). Both are, to some extent, linked to the declining ability of the body to repair and maintain body tissues with age (Campisi 1998; Gilchrest & Yaar 1992; Jenkins 2002).

11.2.3 Extrinsic skin ageing.

Extrinsic ageing occurs in a large part due to exposure to ultraviolet light, which damages skin cells and reduces their ability to replicate accurately (Gilchrest & Yaar 1992; Jenkins 2002). UV photodamage is thought to have a large effect on visible aspects of skin ageing (roughly 80%

(Gilchrest, 1992) and leads to a loss of elasticity, roughness or dryness of the skin, mottled pigmentation and deep wrinkles (Kligman & Kligman 1986). Most of these features are the result of damage done by UV radiation to the production of collagen in the skin, which promotes a decline in cell matrix quality and to the skin's elastic fibre network (Jenkins 2002). An additional source of extrinsic ageing is exposure to free radicals in the environment which causes oxidation in the cells leading to a steady decline in collagen production and thereby a degradation in the elasticity and thickness of the cellular matrix in the skin (Podda & Grundmann-Kollman 2001).

Extrinsic skin ageing due to UV or free radical exposure is not directly linked to developmental speed, although there is a possibility that cellular senescence leads to a deterioration in tissue repair and a decline in skin remodeling ability due to reduced levels of collagen production with age (Gerstein et al. 1993) see below). Effects of photodamage may therefore become more severe with age (Jenkins 2002). In either case, given the nature of the samples in this thesis (18-25 year old, Caucasian undergraduates from the University of St Andrews) differences in UV exposure are unlikely to be particularly pronounced.

11.2.4 Intrinsic Skin Ageing

The process of cellular senescence leads to an arrest of cellular growth in the dermis (Jenkins, 2002; Hayflick, 1965) leading to a decline in proliferation of keratinocytes, fibroblasts and melanocytes that causes the major phenotypic changes in human skin associated with ageing (Fenske & Lober 1986; Jenkins 2002); the changes in pigmentation due to decreased or irregular melanin production and the overall strength and elasticity of the skin, due to decreased keratin production and altered fibroblast activity. Senescent fibroblasts begin to produce enzymes which inhibit collagen production, whereas presenescent fibroblasts promote the production of collagen. The resulting decline in skin collagen leads to a loss of elasticity of skin and a steady thinning of the dermis, both of which are visible cues of ageing. Furthermore, skin cell senescence is associated with a decreased level of cell apoptosis (genetically controlled death), leading to an accumulation of

senescent cells with associated differences in function and phenotype in the dermis (Fenske & Lober 1986), leading to increasing levels of phenotypic change in skin with advancing age.

11.2.5 Ageing and Skin Texture

The processes of both extrinsic and intrinsic ageing impact on skin texture. The loss of collagen in each causes the skin to lose tautness and to become less smooth, while the fine wrinkles and crows feet associated with intrinsic ageing and the deep wrinkles associated with extrinsic ageing are both obvious, skin texture cues to ageing. The mottled pigmentation of intrinsic ageing, caused by cellular senescence in the melanocytes, also cause skin texture to appear less even. Smooth, evenly coloured skin is associated with youth, while coarser, patchy skin is associated with increased age.

11.2.6 Skin Phenotype and Life History Trajectory

Although chronological age is closely associated with cellular senescence (Campisi 2000), the important factor here is that deterioration in skin appearance and function is linked to a decline in skin cell replicative ability; a decline in somatic growth and tissue repair. As such, this process is closely linked to the central life history trade off between gamete formation and maintenance of bodily tissues (Chisholm 1993; Stearns 1992; Stearns 1977). Early puberty should be diagnostic of a life history trajectory associated with increased investment in reproductive effort at the expense of tissue repair. As such, early puberty should be visible in the skin, with faster developing individuals showing earlier deterioration in skin function and appearance, although when such processes should occur is unclear.

11.2.7 Testosterone and Skin Quality.

The benefits to males of increased testosterone levels, increased dominance enhancing behaviours and intrasexually competitive ornaments, may be balanced by immunosuppressive effects of the androgen which leave a high-testosterone male less able to withstand environmental assault

(Folstad & Karter 1992; Olsson et al. 2000; Thornhill & Gangestad 1999). Evidence for the immunosuppressant effects of testosterone is far from equivocal. In birds, testosterone has been shown to correlate positively with parasite load (Saino & Moller 1997), as would be predicted if testosterone handicapped the immune system, although this result was not replicated by Weatherhead et al. (1993) who found no relationship between parasite load and testosterone in birds. Furthermore, Saino et al. (1995) found no relationship between testosterone levels and lymphocyte count (lymphocyte cells are vital to immune system functionality), although Zuk et al. (1995) showed that exogenous testosterone decreased lymphocyte counts, consistent with the immunohandicap hypothesis. Hasselquist et al. (1999) show that decline in immunoresponse associated with high testosterone in red-winged blackbirds (*Agelaius phoeniceus*) is dependent on the testosterone-induced increase in glucocorticoids rather than testosterone itself, while Da Silva (1999) suggests that testosterone, oestrogen and glucocorticoids are involved in complex 3 way interactions with immune system functionality.

If testosterone does act as an immunosuppressant, either directly or indirectly, then this effect may be visible in the skin. The skin's ability to defend itself against environmental assault, including that from parasites and pathogens, is directly linked to extrinsic skin ageing, with lower immunocompetence being associated with increased skin age (Thivolet & Nicolas 1990)

The following hypothesis is advanced:

Men reporting early puberty should have a distinct skin phenotype from men reporting later puberty, owing either to the decreased investment in tissue maintenance implied by their life history trajectory or to the deleterious effects of testosterone on immune system functionality .

11.3 Automatic Analysis of Skin Texture using Gabor Wavelets

Hierarchical decomposition of images using wavelets has been shown to be an efficient tool for the description of variation in pixel intensity of an image while maintaining the maximum amount of information about that image (Stollnitz et al. 1995). Wavelets are extensively used in computer graphics to describe surface texture of objects, and have been successfully used by Tiddeman et al. (2001) to apply realistic skin texture to composite facial images. This analysis uses the sinusoidal Gabor Wavelet function as described by Tiddeman et al. (2001). Gabor Wavelets have been shown to have substantial homology with mammalian visual processing (Daugman 1980). As such, the results provided by a Gabor Wavelet analysis are likely to be extremely close to a direct quantification of a visual assessment of texture by a human.

Gabor Wavelets are convolved with images at four rotations to a number of spatial scales (seven in this analysis), with resolution decreasing at each step (Tiddeman et al. 2001). Average power or amplitude of periodic fluctuation in pixel intensity are returned for each rotation for each spatial scale. This provides an average level of edge strength of structures at the different scales and, consequently, a measure of the texture the image as caused by irregularities in colouration or shade. In terms of skin, high resolution features are likely to be pores, fine lines or crow's feet, low resolution features are likely to be heavy wrinkles or scars while freckles or irregular colouration are likely to occupy mid-range spatial scales.

11.4 Methods

The sample in the following experiments contains the same participants from chapters 7, 8 and 9. Salivary testosterone, 2D:4D, rated appearance and puberty variables were gathered as described in these chapters.

11.4.1 Texture Analysis.

Photographs were taken as described in chapter 7. Photographs of 42 male participants were normalised (but not warped) for interpupillary distance to a standard image to allow patches to be cut from the same area on each face. These images were saved in .tif format and were 2848 x 3646 pixels. 350 x 350 pixel patches were cut from the cheek of each face, positioned so as to avoid as much of the beardline and jawline as possible (see fig 11-1) and saved as separate .tif images using MATLAB. The patches were subjected to Gabor wavelet analysis using Psychomorph. Analysis took place at 4 rotations to 7 spatial scales. For each rotation in each spatial scale a mean value of edge strength within the whole skin patch was returned (see Tiddeman et al., 2001), giving 28 texture components for each patch.

The number of variables was reduced using factor analysis with varimax rotation. 3 interpretable factors with eigenvalues greater than 1 emerged. Table 11-1 and figure 11-2 summarise the factor loadings. The three factors load distinctly on different spatial scales, and appear to represent fine scale, mid range, and coarse scale features respectively. These terms will be used to identify the factors in the forthcoming analysis and discussion. In total the factors accounted for 88.1% of the variance in texture the patches. The five highest and lowest scoring patches for each factor were visually inspected for biological meaning (see figure 11-3 for highest and lowest scoring patches for each factor). The fine scale factor appears to represent pore size, with high scoring skin patches having noticeable larger pores than lower scoring skin patches. The midrange factor corresponds to general 'roughness' of texture and mottled pigmentation, with high scoring patches having rougher and more mottled skin. The coarse scale factor is not easily visualised, although there is a possibility for the high scoring patches to have more fine hairs and be more oily (high shine) than the low scoring patches.

11.4.2 Colour Analysis

Mean L* (luminance), a* (green-red) and b* (blue-yellow) values were calculated for each patch using MATLAB. [L* mean = 66.16 , SE = .81, a*mean = 16.61, +/- .40, b*=14.37, SE = .30].

11.5 Results

11.5.1 Puberty and skin texture in men

Shapiro Wilk tests reveal that all three skin texture factors are normally distributed ($p > .10$), while age of first shave, relative puberty speed and mean 2D:4D are non normally distributed ($p < .006$).

Mean salivary testosterone shows a trend towards non-normality ($p = .09$). Consequently spearman's rank order correlations were used in the following analysis. 2 men did not give more than 1 saliva sample, so no mean salivary testosterone could be calculated. The sample drops by 2 for this variable.

Puberty speed does not correlate with any skin texture factor [fine scale: $r = -.17$, $n = 40$, $p = .31$; midrange: $r = .07$, $n = 40$, $p = .67$; coarse scale: $r = .07$, $n = 40$, $p = .67$]. Age of first shave correlates with the midrange factor [$r = -.37$, $n = 42$, $p = .02$, see figure 11-4], but not with either of the other two factors [fine scale: $r = .04$, $n = 41$, $p = .83$; coarse scale: $r = .13$, $n = 42$, $p = .62$].

11.5.2 Puberty and skin colour in men.

Mean L* and a* values for the skin patches are normally distributed [Shapiro Wilk, $p > .37$], while b* values violate an assumption of normality [$p < .01$].

Spearman's rank order correlations show that L* correlates negatively with relative puberty speed [$r = -.36$, $n = 40$, $p = .02$, see figure 11-5] and shows a positive, non significant relationship with age of first shave [$r = .26$, $n = 41$, $p = .1$], suggesting that early developing men have darker skin. Neither a*

[first shave: $r=-.08$, $n=41$, $p=.62$; relative puberty speed: $r=.03$, $n=40$, $p=.87$] nor b^* [first shave: $r=-.08$, $n=41$, $p=.63$; relative puberty speed: $r=-.12$, $n=40$, $p=.46$] correlate with either puberty variable.

No patch colour variable correlates with chronological age [L^* : $r=-.02$, $n=42$, $p=.89$; a^* : $r=.15$, $n=42$, $p=.33$; b^* : $r=.02$, $n=42$, $p=.91$],

11.5.3 Rated Appearance and Skin Texture in Men.

Face ratings gathered by independent raters as described in chapter 6. All face ratings are normally distributed according to Shapiro-Wilk tests [$p>.4$]. Pearsons correlations are used in the following analysis.

Rated attractiveness does not correlate with any skin texture factor [fine scale: $r=.09$, $n=35$, $p=.61$; midrange: $r=-.19$, $n=35$, $p=.26$; coarse scale: $r=.11$, $n=35$, $p=.52$]. Neither does rated health [fine scale: $r=.16$, $n=35$, $p=.35$; midrange: $r=-.02$, $n=35$, $p=.93$; coarse scale: $r=.17$, $n=35$, $p=.34$] or rated masculinity [fine scale: $r=.22$, $n=35$, $p=.21$; midrange: $r=.15$, $n=35$, $p=.37$; coarse scale: $r=-.29$, $n=35$, $p=.10$]. The relationship between biological age (perceived minus real age) and the skin texture factors was investigated partialling out chronological age. This revealed that biological age correlates positively with the midrange skin texture factor [$r=.41$, $n=32$, $p=.02$, see figure 11-6]. This may be a replication of the finding of Jones et al. (2004a) who report that apparent skin health correlates with visually assessed skin texture. Biological age also shows a positive trend with the coarse scale texture factor [$r=-.23$, $n=32$, $p=.09$] but does not correlate with the fine texture factor [$r=.17$, $n=32$, $p=.33$].

11.5.4 Rated appearance and Skin Colour in Men

Pearson's product moment correlations show that L^* shows a negative trend with attractiveness [$r=-.3$, $n=35$, $p=.5$] and a positive trend with a^* [$r=.30$, $n=35$, $p=.30$]. Spearman's rank order correlation shows that b^* does not correlate with attractiveness rating [$r=.18$, $n=35$, $p=.29$]. L^* does not

correlate with either rated health [$r=-.27$, $n=35$, $p=.11$] or rated masculinity [$r=-.9$, $n=35$, $p=.59$], a^* does not correlate with rated health, although is almost showing a positive trend [$r=.29$, $n=35$, $p=.10$], but does correlate with rated masculinity [$r=.43$, $n=35$, $p=.01$, see figure 11-7]. b^* does not correlate either with health [$r=.20$, $n=35$, $p=.25$] or with rated masculinity [$r=.18$, $n=35$, $p=.31$]. Partial correlations controlling for chronological age show that biological age does not correlate with any colour variable [L^* : $r=.18$, $n=31$, $p=.33$; a^* : $r=-.02$, $n=31$, $p=.93$; b^* : $r=.12$, $n=31$, $p=.48$].

11.5.5 2D:4D, Salivary Testosterone and Skin Texture in Men

Shapiro Wilk tests show that both average salivary testosterone and average 2D:4D violate an assumption of normality [$p>.05$]. Spearman's rank order correlations are used in the following analysis.

Mean 2D:4D does not correlate with any skin texture factor [fine scale: $r=-.25$, $n=39$, $p=.13$; midrange: $r=.02$, $n=39$, $p=.92$; coarse scale: $r=.03$, $n=39$, $p=.85$]. Salivary testosterone correlates negatively with the coarse scale texture factor [$r=-.31$, $n=40$, $p=.05$; see figure 11-8] but not with either of the other two [fine scale: $r=.01$, $n=40$, $p=.95$; midrange: $r=.12$, $n=40$, $p=.45$].

11.5.6 2D:4D, Salivary Testosterone and Skin Colour in Men

Spearman's rank order correlations show that mean salivary testosterone does not correlate with L^* [$r=-.21$, $n=40$, $p=.19$], a^* [$r=-.03$, $n=40$, $p=.59$] or b^* [$r=.97$, $n=35$, $p=.56$]. Mean 2D:4D does not correlate with L^* [$r=-.07$, $n=40$, $p=.66$], a^* [$r=.04$, $n=40$, $p=.82$] or b^* [$r=.09$, $n=40$, $p=.58$].

Skin Colour and Skin Texture.

Associations between colour values and texture factors may be useful in identifying the biological meaning of the skin texture factors. Pearson's product moment correlations show that the fine scale factor correlates positively with L^* [$r=.32$, $n=40$, $p=.04$; see figure 11-9] and a^* [$r=.37$, $n=40$,

$p=.02$, see figure 11-10], while Spearman's rank order correlations reveal no relationship between the fine scale factor and b^* [$r=.17$, $n=40$, $p=.28$]. The midrange factor does not correlate with any colour variable [L^* : $r=.1$, $n=40$, $p=.54$; a^* : $r=-.1$, $n=40$, $p=.54$; b^* : $r=.12$, $n=40$, $p=.44$]. The coarse scale factor correlates positively with L^* [$r=.34$, $n=40$, $p=.03$; see figure 11-9] but not with a^* [$r=-.04$, $n=40$, $p=.82$] or b^* [$r=.24$, $n=40$, $p=.14$].

11.5.7 Summary of Results

Age of first shave and biological age both have a positive relationship with the midrange skin texture factor which is consistent with the hypothesis that the more rapid developmental trajectory of early puberty men is apparent in their skin. According to the visual analysis of the skin texture factors, this means that earlier developing men have rougher and more mottled skin than later developing men. The fact that men who are rated as looking older for their chronological age share this feature is consistent with the prediction that the accelerated ageing of early developing men is apparent in their skin. Men reporting early puberty are also shown to have darker skin than later developing men. Skin luminance is not affected by age and is not related to biological age, so this phenotypic difference may be independent of an accelerated ageing trajectory. Faces with darker skin patches tend to be rated as being less attractive, while increased a^* (redness) in a skin patch is associated with increased facial attractiveness. There is no relationship between redness and health. Increased redness is associated with facial masculinity, although there is no relationship between redness and either salivary testosterone or 2D:4D which might be expected if theories linking redness to dominance through the action of testosterone apply to the human face (Hill & Barton 2005). The midrange skin texture factor is negatively related to salivary testosterone, suggesting that testosterone has an effect on skin phenotype. Given that the midrange factor is associated with increased roughness and mottled pigmentation, which are generally associated with increased

chronological age (Fisher et al. 2002) and hence decreased skin quality, this relationship is in the opposite direction from that predicted in the original hypothesis.

11.6 Controlling for Variation in Lighting Conditions

The correlation between age of first shave and luminance could be an artefact of the photography process. Although pains were taken to control the lighting conditions under which photographs were taken, it is possible that variation in flash intensity would change the amount of light reflected by an individual face and thereby influence the luminance of the skin patch. This is of particular concern since visual inspection of the skin texture factors suggests a difference in lighting conditions between the lowest scoring and highest scoring skin patches for the coarse skin patch factor, a possibility confirmed by the positive correlation between L^* and the coarse scale factor.

In order to control for this, a small, 50 x 50 pixel patch was cut from the top left hand corner of each image before normalization. This area contained only the uniform grey background behind each participant. Average luminance was calculated for each background patch using MATLAB. For the whole sample, mean L^* was 54.4 +/- 1.67, ranging from 33.93 to 78.95. If the correlations discovered so far are artifacts of the lighting conditions, then background luminance should show similar relationships.

Background luminance shows a positive trend with the midrange skin texture factor [$r=.82$, $n=40$, $p=.08$] and with rated femininity [$r=.29$, $n=40$, $p=.07$] but does not correlate with any other examined variable (including patch colour variables) [$p>.11$ in each case]. This is sufficient cause to suspect the influence of absolute lighting conditions on at least some of the relationships reported so far.

All correlations were repeated controlling for background luminance using partial correlations.

11.7 Results 2: controlling for background luminance variation.

11.7.1 Puberty and Skin Phenotype

Following the partialling out of background luminance, no skin texture factor correlates with either age at first shave [fine scale: $r=.01$, $n=37$, $p=.96$; midrange: $r=-.23$, $n=37$, $p=.17$; coarse scale: $r=.12$, $n=37$, $p=.48$] or relative speed of puberty [fine scale: $r=-.15$, $n=37$, $p=.35$; midrange: $r=.04$, $n=37$, $p=.79$; coarse scale: $r=-.05$, $n=37$, $p=.77$]. The correlation between relative speed of puberty and patch luminance has become marginally stronger [$r=-.37$, $n=37$, $p=.02$] while the relationship between age of first shave and skin patch luminance has become significant [$r=.34$, $n=37$, $p=.03$]. Correlations between skin patch a^* [first shave: $r=-.07$, $n=37$, $p=.66$; relative puberty speed: $r=-.02$, $n=37$, $p=.92$] and b^* [first shave: $r=-.09$, $n=37$, $p=.60$; relative puberty speed: $r=-.18$, $n=37$, $p=.28$] and puberty variables remain non-significant.

11.7.2 Rated Appearance and Skin Phenotype

Partialling out background luminance does not effect the lack of correlation between skin texture factors and rated attractiveness [fine scale: $r=.10$, $n=32$, $p=.62$; midrange: $r=-.20$, $n=32$, $p=.25$; coarse scale: $r=.12$, $n=37$, $p=.48$], health [fine scale: $r=.16$, $n=32$, $p=.35$; midrange: $r=-.02$, $n=32$, $p=.93$; coarse scale: $r=.12$, $n=37$, $p=.48$] or masculinity [fine scale: $r=.18$, $n=32$, $p=.30$; midrange: $r=.06$, $n=32$, $p=.72$; coarse scale: $r=-.23$, $n=32$, $p=.19$]. The correlation between L^* and attractiveness is maintained [$r=-.35$, $n=32$, $p=.04$], the relationship between a^* and rated attractiveness has become a stronger, positive trend [$r=.30$, $n=32$, $p=.08$], while b^* shows a positive trend with rated attractiveness [$r=.33$, $n=32$, $p=.06$]. Partialling out both background luminance and chronological age removes the trend between the coarse scale factor and biological age [$r=-.29$, $n=31$, $p=.13$]. The correlation between the midrange factor and biological age is remains [$r=-.37$,

$n=31, p=.03$]. There is still no relationship between the fine scale factor and biological age [$r=.15, n=31, p=.41$].

11.7.3 2D:4D, Salivary Testosterone and Skin Phenotype

Salivary testosterone no longer correlates with any skin texture factor when background luminance is partialled out [fine scale: $r=-.03, n=36, p=.96$; midrange: $r=.11, n=36, p=.50$; coarse scale: $r=-.26, n=36, p=.12$]. Relationships between salivary testosterone and skin patch colour remain non significant [L^* : $r=-.24, n=36, p=.15$; a^* $r=-.01, n=36, p=.97$; coarse scale: $r=-.11, n=36, p=.51$]. The relationships between mean 2D:4D and any skin texture factor remain non-significant [fine scale: $r=-.24, n=37, p=.14$; midrange: $r=.05, n=37, p=.21$; coarse scale: $r=-.14, n=37, p=.40$], as do the relationships between mean 2D:4D and skin colour variables [L^* : $r=-.06, n=37, p=.71$; a^* $r=.09, n=37, p=.58$; coarse scale: $r=.01, n=37, p=.58$].

11.8 Summary and Discussion.

The new results show that there is a strong likelihood that many of the earlier reported skin factor correlates were affected by variation in flash intensity during the photography procedure.

Controlling for background luminance reveals that, although there is a relationship in this sample between the midrange skin texture factor and biological age, in that poor agers appear to have rougher and more mottled skin, this seems unrelated to pubertal timing. No feature of skin texture identified in this experiment has a relationship with reported puberty speed, so the hypothesis that investment in reproductive effort at the expense of tissue maintenance would cause difference in skin phenotype in terms of texture is not supported. Although testosterone appears to have a relationship with the midrange skin texture factor, this effect vanishes once background luminance is controlled for, suggesting that this is an artefact of flash intensity variation, and offering no support for the hypothesis that testosterone would have a deleterious effect on skin texture owing to its immunosuppressant action. There is, however, a correlation between skin luminance and pubertal timing variables, showing that men reporting earlier puberty in this sample have darker

skin. This offers some support to the general hypothesis that skin phenotype is effected by pubertal timing, although not in the way predicted. The lack of relationship between either salivary testosterone or 2D:4D and skin luminance suggests that the difference in luminance between early and late developers is not under current or foetal androgenic control, so alternative explanations must be sought.

Absolute variation in ambient luminance has been controlled for by partialling out background luminance of each photograph. Consequently, the next candidate for variation in skin luminance must be skin reflectivity. Visual inspection of high luminance skin patches reveals that light skin appears more oily than darker skin. Skin oiliness is the result of sebum producing activity of the sebaceous glands, which are under androgenic control (Eady & Bojar 2001).

11.8.1 Sebaceous gland development and the production of sebum.

Human sebaceous glands are fully developed by the 15th week of gestation (Serri & Huber 1963) and are indistinguishable from adult sebaceous glands at this point (Pochi & Strauss 1974). Their uterine function appears to be to contribute to the *vernix caseosa*, the waxy substance which coats the skin of foetuses and neonates (Pochi & Strauss 1974). After birth, sebaceous gland activity declines and the glands enter a stage of dormancy, remaining small in size (Strauss et al. 1962; Strauss et al. 1978) and producing small but increasing quantities of sebum (Pochi et al. 1962; Pochi et al. 1979) throughout childhood. Although the hormonal changes of puberty are generally associated with maximum sebum production (Pochi & Strauss, 1974), sebaceous gland activity is actually reinitiated somewhat earlier, during adrenarche (maturation of the adrenal glands), occurring at roughly 6 -10 years of age in both sexes. (Eady & Bojar 2001; Pochi et al. 1962; Pochi et al. 1979). Sebaceous gland activity rises steadily from adrenarche until the late teens (see figure 11), at which point sebum production stabilises and remains relatively stable until it declines at around age 80 (Pochi et al., 1979). Sebum production is apparently initiated and controlled by the action of testosterone; castrated men produce markedly lower levels of sebum than non-castrated

men (Pochi, 1962;Hamilton, 1963), while the administration of testosterone to castrated males increases sebum production (Pochi et al. 1962). Exogenous testosterone also increases the amount of sebum produced by children (Strauss et al. 1962).

Testosterone does not correlate with skin luminance in this sample, so the androgenic influence on skin oiliness through the action of sebum is not apparent here. Sebum production increases steadily from adrenarche until full maturity is reached (Pochi et al. 1979). There is, therefore, a possibility that individuals reaching puberty early show a smaller increase in sebum production than those developing late, since the increase in production is curtailed earlier. By contrast, the later developing males would continue producing increased amounts of sebum until their own production level is stabilised by puberty. This is dependent on an assumption that adrenarche occurs at similar points in the development of men, independently of differences in pubertal timing. Adrenarche and puberty do not appear to be causally linked (Parker 1991; Saenger & Reiter 1992); adrenarche is a permissive factor for puberty, but is not necessary for its initiation (Parker 1991) and girls showing precocious adrenarche often develop normally thereafter and show pubertal development within normal age range (Saenger & Reiter 1992). It is therefore possible for the men in this sample to have shown little variation in adrenarche, the point at which sebum production begins to rise, while showing variation in pubertal timing, the point at which sebum production level is stabilised. Consequently, it is possible that the increased luminance shown by later developing men in this sample is due to the increased length of time between adrenarche and puberty they have experienced compared to the earlier developing men.

Whether or not the decreased production of sebum can be considered a cost of early development is not clear. Sebum is a major route for the delivery of vitamin E (Thiele et al. 1999) and other antioxidants (Passi et al. 2002; Thiele 2001) to the surface of the skin, which is thereby protected from the harmful effects of oxidative stress from the environment (Thiele et al. 1999). Sebum also has bactericidal and fungicidal properties (Skewes 1996). Men producing less sebum may therefore

be less well protected against deleterious agents in the environment such as free-radicals, which can impact negatively on skin ageing (see above). If this is the case, then the true cost to skin quality of early development would be increased extrinsic ageing, which would be most pronounced later in life. At the age of the current sample (18-24 years) the early developing men may still be reaping the benefits of their developmental trajectory (increased attractiveness and masculinity, see chapter 6), while their increased susceptibility to extrinsic ageing would be a cost later in life.

11.9 Conclusion

Skin texture is related to biological age, although not developmental trajectory as indicated by retrospective recall of puberty. Men in this sample reporting earlier puberty do not show the hypothesised phenotypic difference in skin texture, but do show a phenotypic difference in terms of skin luminance with earlier developing men having darker skin. This difference is resilient to the Skin oiliness is a result of sebum production. control of background luminance, suggesting that it is due to the reflectivity of the skin, caused by skin oiliness. Since sebum offers protection to the surface of the skin against deleterious environmental agents which lead to extrinsic ageing, it is possible that early developing men will be more susceptible to extrinsic ageing. This difference may only become apparent later in life, when earlier developing males will show signs of increased extrinsic ageing.

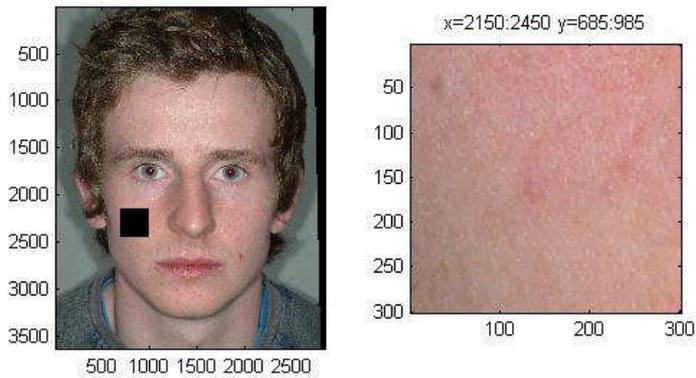


Figure 11-1: Location of Skin Patches

		FACTORS		
		1	2	3
% Variance explained		45.10	22.97	20.01
<i>Resolution_rotation</i>				
High Resolution, fine texture	1_1	0.89		0.32
	1_2	0.86		0.39
	1_3	0.91		0.32
	1_4	0.91		0.32
	2_1	0.96		
	2_2	0.93		
	2_3	0.96		
	2_4	0.95		
	3_1	0.90	0.32	
	3_2	0.92		
	3_3	0.88	0.39	
	3_4	0.92		
	4_1	0.72	0.63	
	4_2	0.80	0.54	
	4_3	0.66	0.70	
	4_4	0.73	0.63	
	5_1		0.86	
	5_2	0.37	0.84	
	5_3		0.86	0.33
	5_4		0.84	0.42
Low Resolution, course texture	6_1		0.40	0.82
	6_2		0.80	0.33
	6_3		0.48	0.79
	6_4		0.31	0.90
	7_1			0.90
	7_2		0.52	
	7_3			0.89
	7_4			0.91

Table 11-1: Loadings (>.30) for the three skin texture factors across different spatial scales (top to bottom: fine to course), and variance explained.

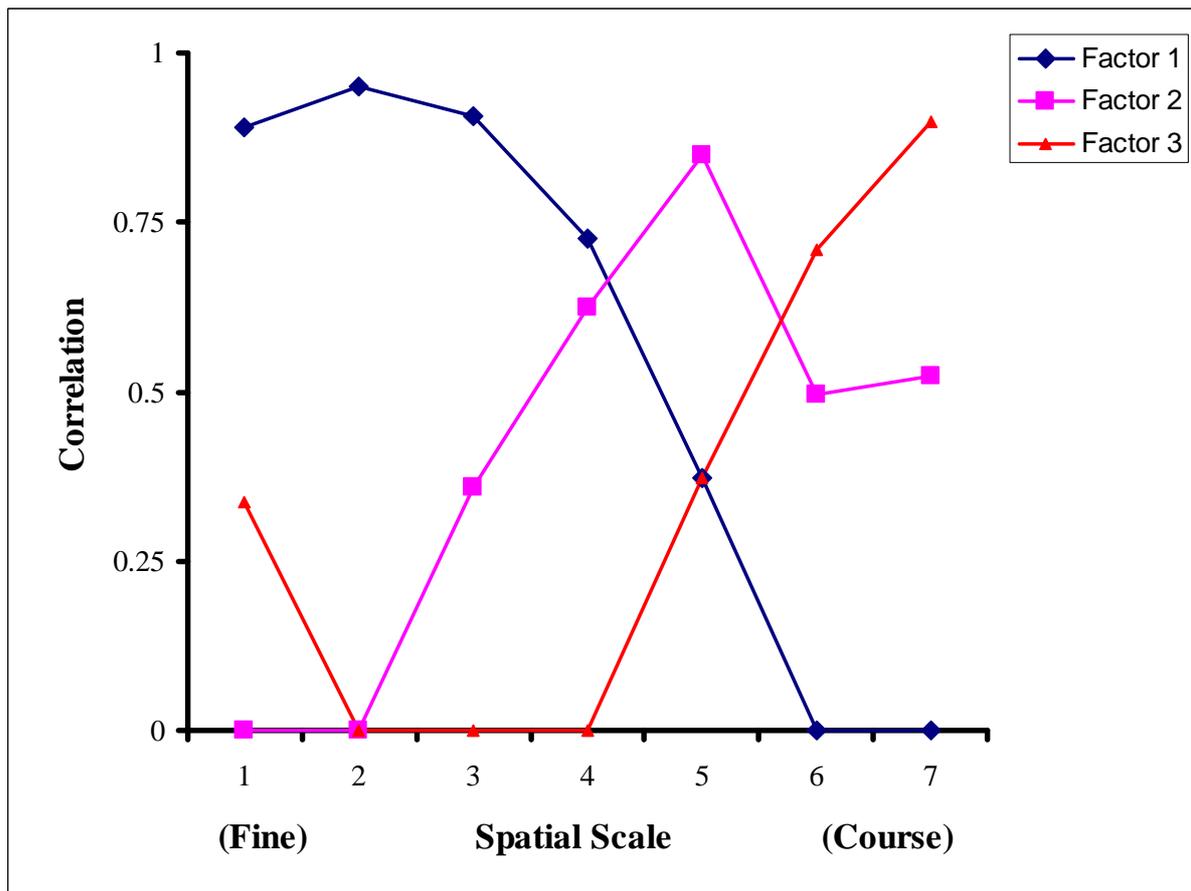


Figure 11-2: Graphical representation of factor loadings. Factor 1 loads most strongly on the fine scale, factor 2 loads on midrange scales and factor 3 on the coarse scale.

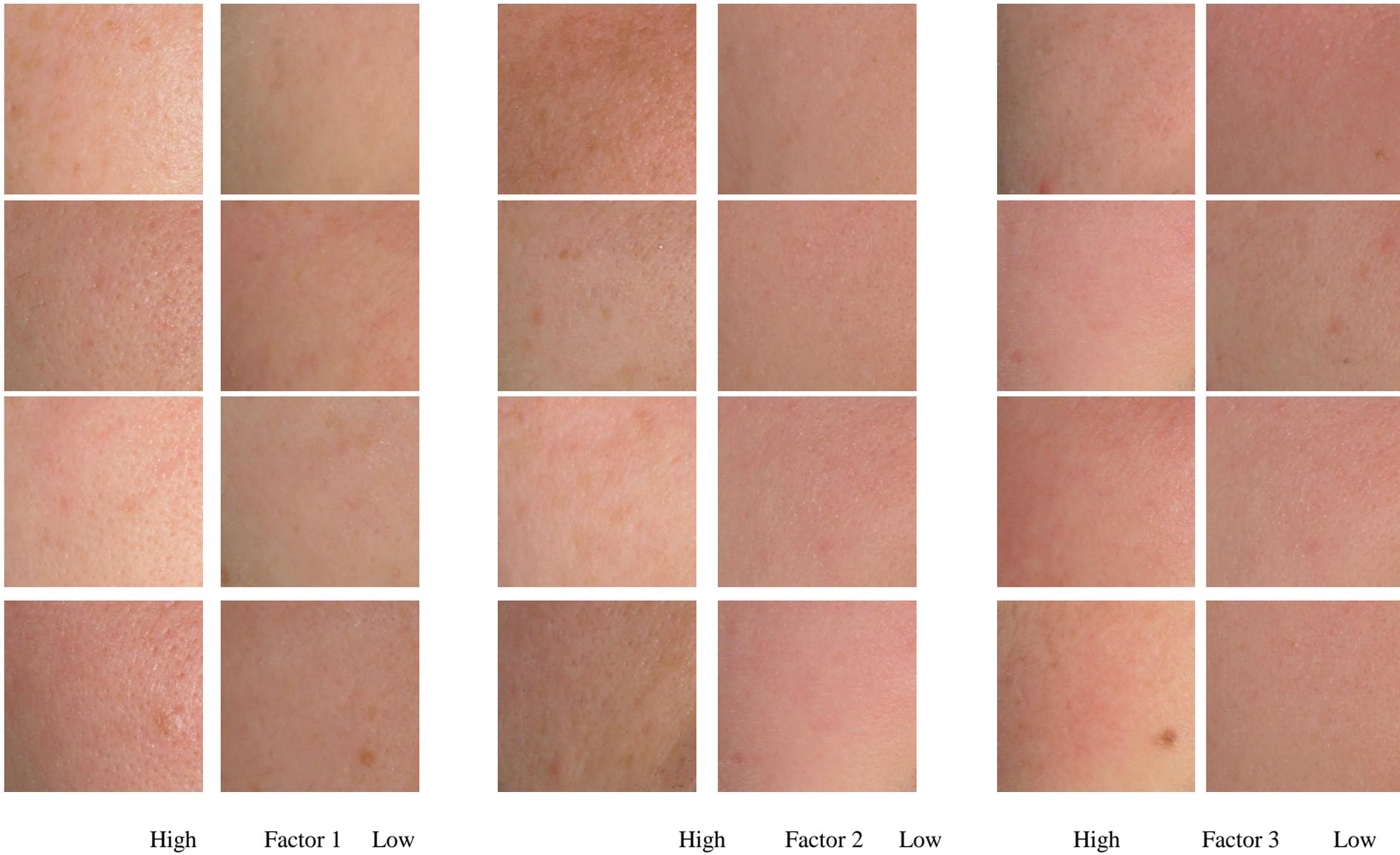


Figure 11-3: *The four highest and lowest scoring skin patches for each skin factor. See text for biological interpretation.*

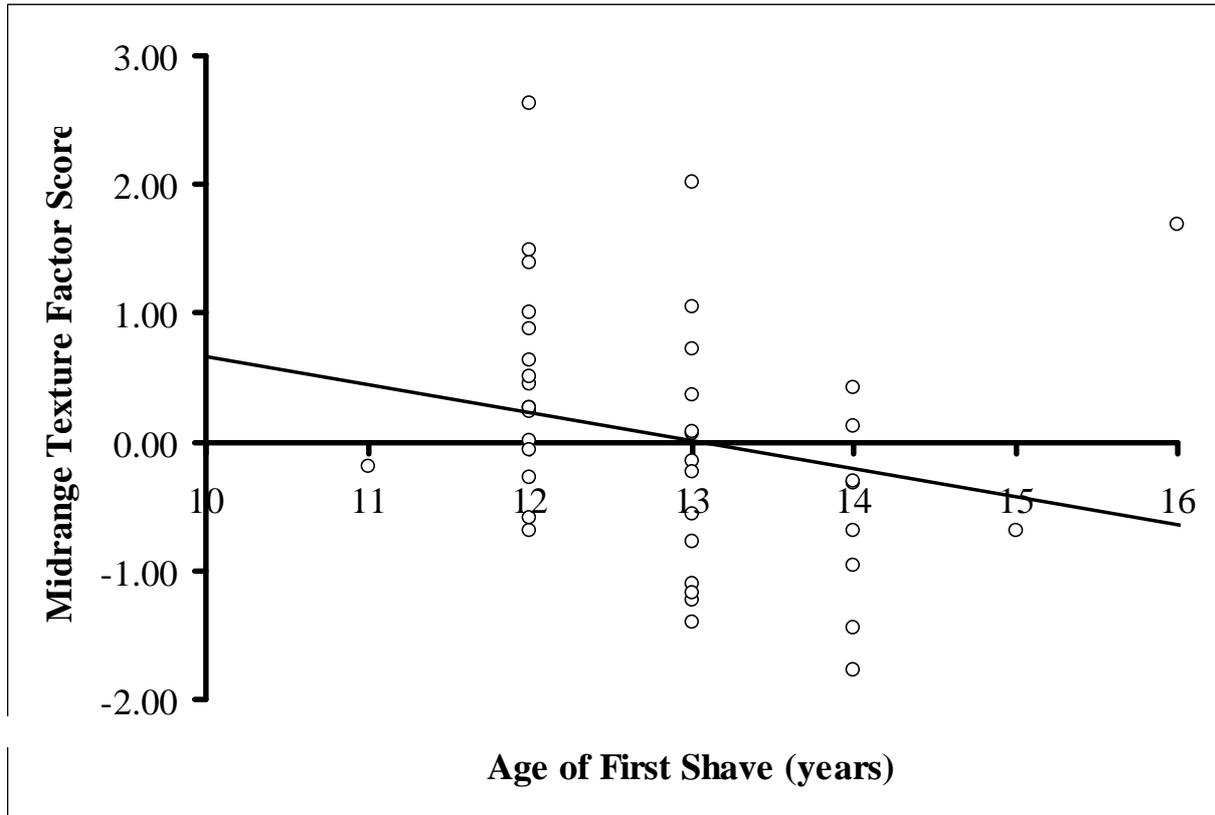


Figure 11-3: Age of first shave shows a negative relationship with midrange texture factor (corresponding to increased 'roughness' and mottled pigmentation of skin) prior to control for background luminance.

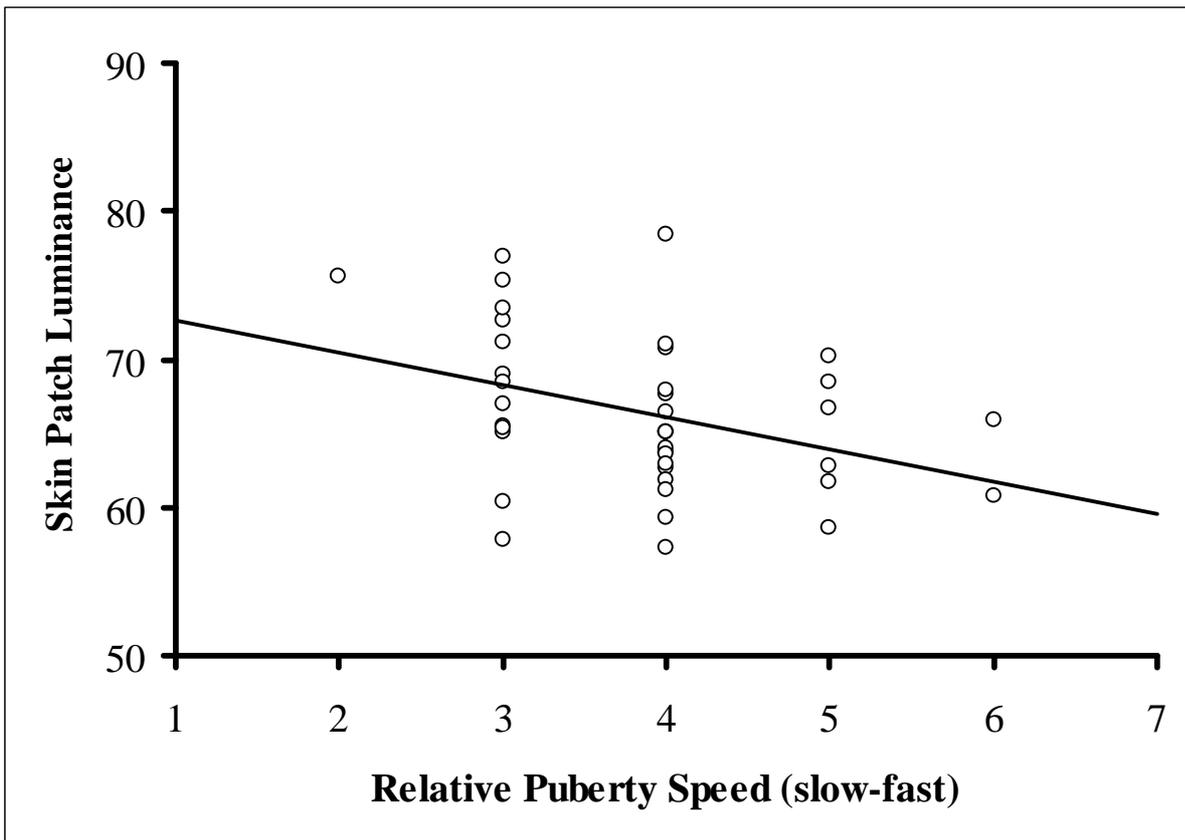


Figure 11-4: Relative puberty speed shows a negative relationship with skin patch luminance, prior to control for background luminance.

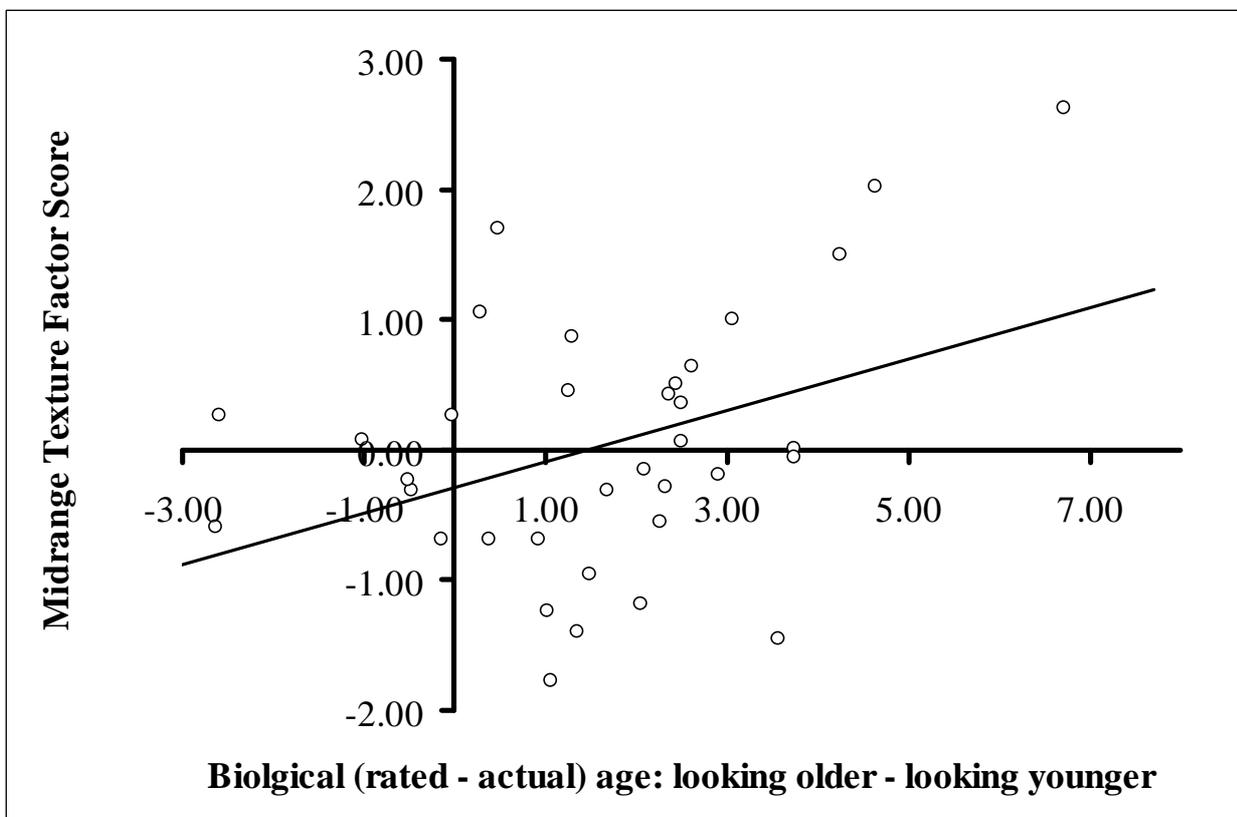


Figure 11-5: Biological age (rated age minus actual, chronological age) correlates positively with the midrange (rough, mottled pigmentation) texture factors. Individuals with a high biological age appear younger than they are.

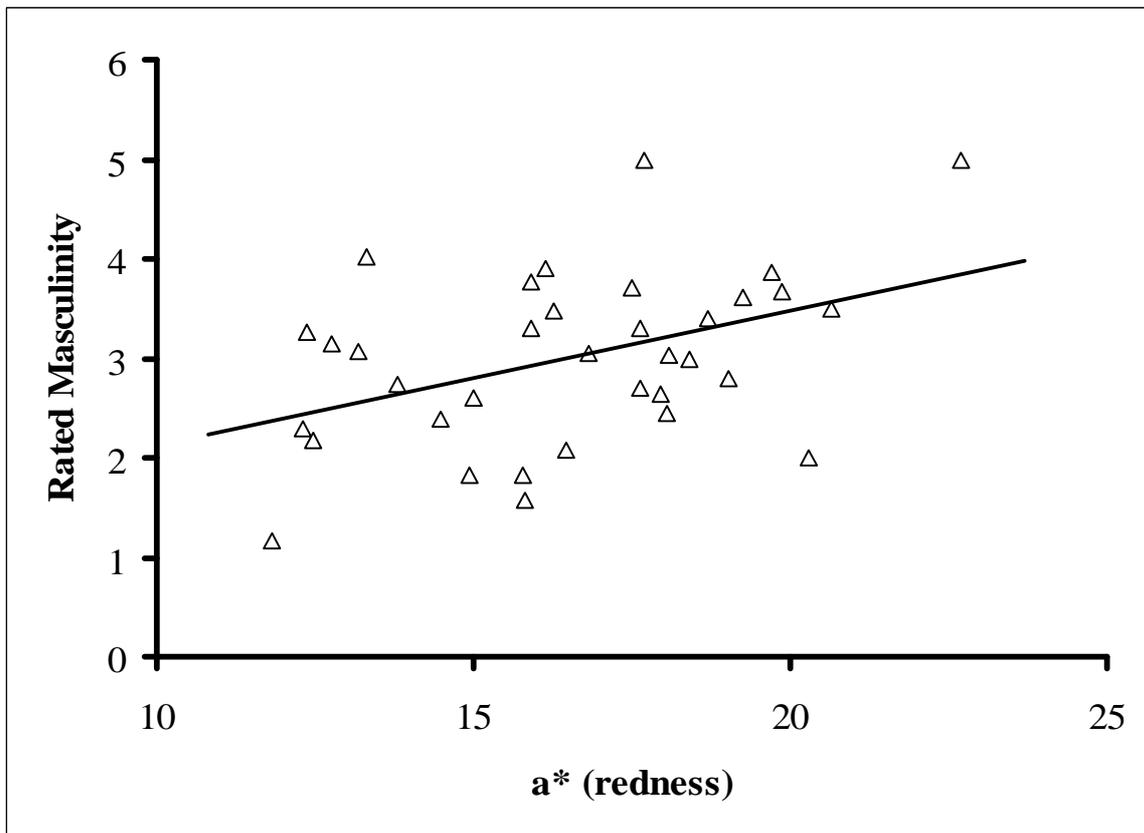


Figure 11-6: Increased redness is associated with increased rated masculinity, prior to control for background luminance.

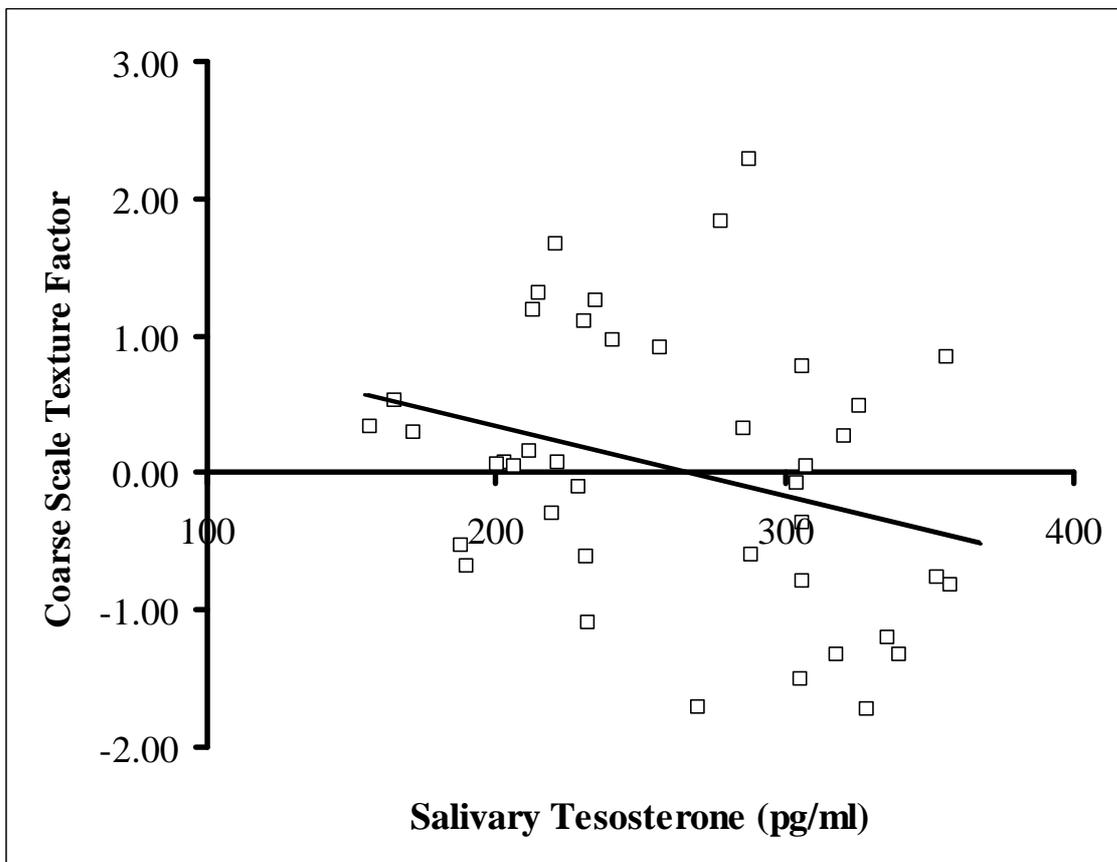


Figure 11-7: Salivary testosterone is negatively associated with the coarse scale texture factor (increased high shine and fine hairs)

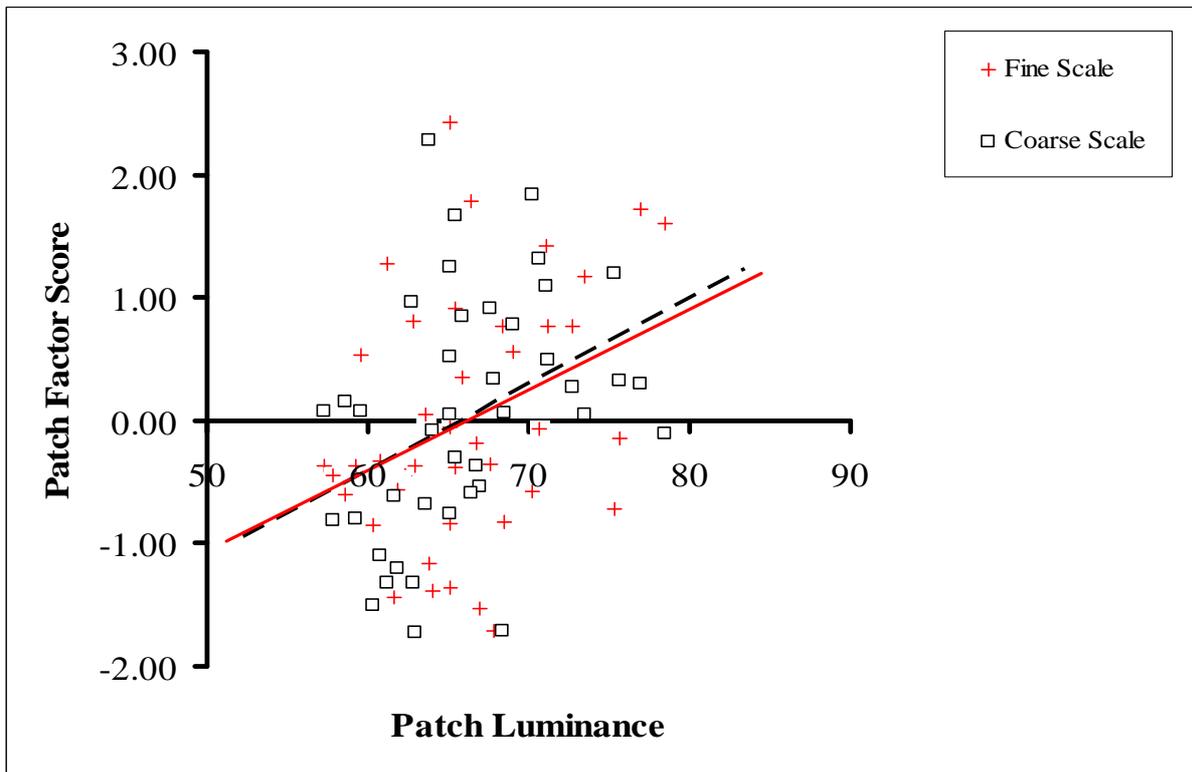


Figure 11-8: Fine scale (increased pore size) and coarse scale (shine and hairs) factors positively correlate with patch luminance.

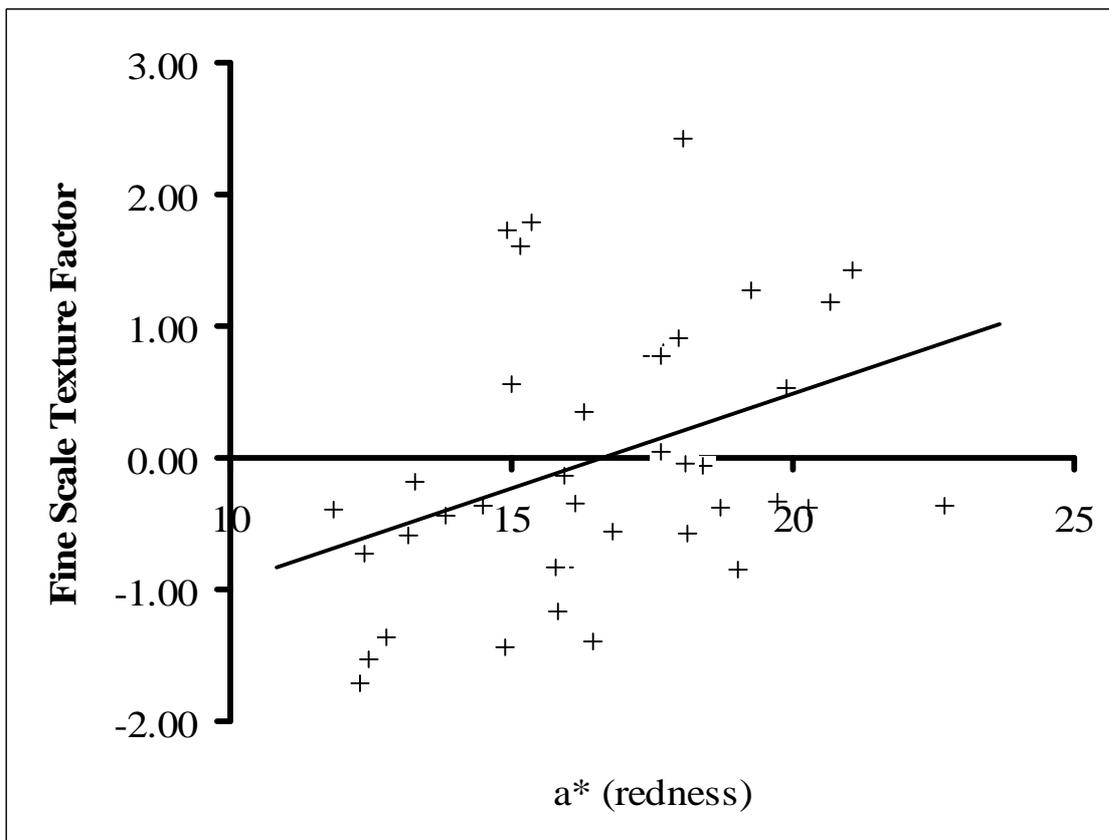


Figure 11-9: The fine scale texture factor correlates positively with increased patch redness.

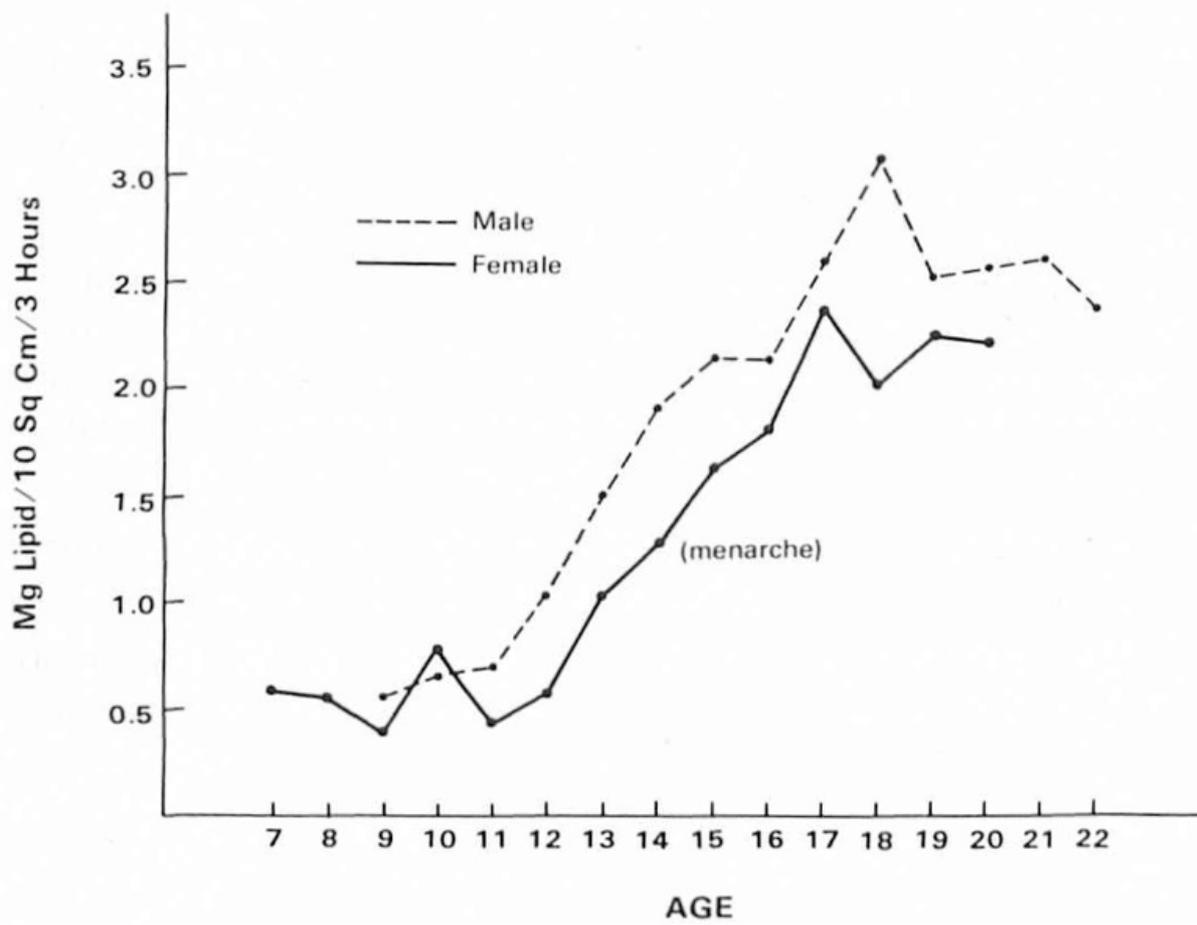


Figure 11-10: The increase in sebum production from childhood to adulthood (from Pochi et al., 1979)

12 Concluding remarks.

12.1 General Discussion

12.1.1 Pubertal Timing and Dominance and their Relationship with Mating Strategy

Chapters 2 and 3 investigated the link between puberty and dominance and human male mating strategy, testing the hypothesis that both early developing and high dominance men will display behavioural traits in line with them being more interested in speedy conception of offspring than in long-term investment in those offspring. These traits should include; increased preferences for short term, casual relationships (unrestricted sociosexuality), a greater preference for signals of femininity or unrestricted sociosexuality in the female face and a tendency to rank physical attractiveness as being an important partner character trait. Chapter 2 reported a relationship between Sociosexuality Orientation Inventory scores and both pubertal timing and dominance in support of a this hypothesis. Both dominant and early developing men were shown to have an unrestricted sociosexuality and, hence, a greater interest in casual sex and short-term relationships than later developing men.

Chapter 3 reported that men scoring high on the Sociosexuality Orientation Inventory prefer cues of unrestricted sociosexuality in the female face, potentially reflecting a male preference for women who are likely to be amenable to the men's own mating strategy; i.e. short-term, casual relationships. Precisely what features signal this trait in the female face is unknown, but independent calibration of the stimulus faces in this chapter confirmed that they contained accurate sociosexuality information. Similarly, while pubertal timing did not show a relationship with male preferences for cues of sociosexuality, high dominance men showed preferences for cues of unrestricted sociosexuality in the female face, in line with predictions that they should be acting to

increase partner numbers by, in this case, identifying women who are likely to tolerate their own unrestricted strategy. That said, neither pubertal timing nor dominance showed the predicted relationship with preferences for femininity in the female face. The null result is, presumably, indicative of a general tendency of men to pick the most feminine-looking face available to them in the absence of any other stimuli, a tendency which may overwhelm any differences between the puberty or dominance groups. Further predictions regarding a tendency of unrestricted sociosexuality or high dominance men to show increased mate guarding are beyond the scope of the current studies, although provide useful and specific predictions for future work (see next section). This may be evidence for a condition dependent effect on male mating strategy (as indexed by Sociosexual Orientation Inventory score and face preferences) with both pubertal timing and dominance playing an important role in its implementation.

Chapter 4 introduced a novel method for the assessment and quantification of mate preferences; the java-based reorderable list. The chapter then proceeded to further examine the dominance-related, condition dependent effect on male mating strategy. In two samples, high dominance men displayed increased 'female-typical' mate preferences, counter to initial predictions. This, combined with the unrestricted sociosexuality of high dominance men from Chapter 2 and the possibility that the phrasing of the question on which mate preferences were reported may bias a participant towards considerations of a long term relationship, suggested the existence of a dual mating strategy in men, whereby a long-term partner is chosen on her ability and desire to raise and care for children while the unrestricted sociosexuality of dominant men, and their preferences for women displaying facial cues of unrestricted sociosexuality, predisposes them to seek multiple, extra-pair copulations. This would be an ideal mating strategy for a man, assuming he has the resources necessary to operate it, since he would then be able to produce *both* high investment and low investment offspring.

Chapter 4 also reported that early developing men prefer and tolerate older partners than later developing men. This may represent a positive assortment for maturity due to the likelihood that

early developing men will have early sexual experiences with older or more mature (hence older seeming) women than later developing men. This may lead to a preference for older women that may track through life, or at least early adulthood.

Chapter 5 again provided more information on the effect of dominance on male mating strategy, this time using pheromones as an indicator of mating strategy. The study relies on an assumption, which has experimental backing, that pheromones are sexually-relevant signals of reproductive condition. Chapter 5 reported that high dominance men are more sensitive and also more averse to a putative female pheromone 1,3,5(10),16-estratetraen-3-ol. The results of this chapter were discussed in terms of avoidance of non-viable matings that would represent a relict, anthropoid adaptation towards avoiding pregnant females. This is a tentative conclusion, based on the only published source of 1,3,5(10),16-estratetraen-3-ol in humans; the urine of pregnant women. A mechanism for the increased olfactory sensitivity of dominant men is also proposed, in that cortisol may be involved in the formation and maintenance of olfactory neurons (as well as in treatment for anosmia). Given that Chapter 9 showed that dominance in men is associated with increased salivary cortisol, this may be a mediating factor in the increased olfactory ability of dominant men. Pubertal timing had no effect on pheromone detection in Chapter 5. If the increased sense of smell is linked to dominance through hormonal action then it is, presumably, plastic as dominance is. By contrast, pubertal timing, once set, cannot be changed so effects of puberty on mating strategy may be evident in more general, more permanent areas, such as sociosexuality, which has been shown to remain largely stable across a lifetime.

12.1.2 Pubertal Timing and Dominance and Appearance

Chapter 6 began the exploration of other effects of pubertal timing. Early development was shown to be associated with more masculine, more attractive looking adult men. Furthermore, the acceleration of development that leads to early puberty may have long-reaching effects on adult appearance in that early puberty males appear to be older than their peers. This accelerated ageing

may represent a cost of early puberty, since looking older than the rest of one's peer group would be likely to have a detrimental effect on the attractiveness of an individual as they age or approach senescence. This idea was returned to in Chapter 11.

Chapter 9 showed that dominant men are more attractive, as theories centering around mate value would predict. However, this attractiveness was shown to be non-facial and more likely to be related to male physique and fitness, since these impact on male bodily attractiveness, as well as on general aspects of attractiveness such as wealth and status. These features are in line with dominance being an emergent property of social influence through resource control or physical intimidation or coercion.

12.1.3 Pubertal Timing, Dominance and Hormones

Chapters 7 and 8 explored the hormonal underpinnings of the increased masculinity of behaviour (i.e. unrestricted sociosexuality) and appearance of early developing men. Men reporting earlier development were shown to have higher levels of salivary testosterone than those reporting later development. This suggests that the differences between early and late developing men may be mediated through the action of the sex hormone, testosterone. There are alternative explanations for this phenomenon, between which this experiment does not differentiate. Either the high testosterone condition leads early developers to behave in a masculine way or the increased masculine-type behaviour leads to elevated testosterone levels, through a tendency to engage in competitive activity more frequently.

This question was to some extent addressed by Chapter 8 where early developing men were shown to have lower digit ratios, indicating exposure to high levels of prenatal testosterone, suggesting that the high adult testosterone of early developing men may be due to uterine hormonal influences. Furthermore, since uterine testosterone (whether produced by the mother or the foetus) positively associates with maternal stress, the finding is possibly indicative of early puberty in human males

being an adaptation towards a stressful environment, as predicted by life history theory. Such a response has already shown to be the case in human females, albeit in response to post-natal stressors. The lack of replication of the relationship between digit ratio and pubertal timing in women suggests that only male developmental trajectory can be adjusted by pre-natal sex hormones. There are plausible reasons for this; first, male foetuses may be more sensitive to testosterone than female foetuses and are, in any case, exposed to significantly more gonadal testosterone *in utero* than female foetuses are. Female foetuses may, therefore, not be exposed to sufficient testosterone nor be sensitive enough to it for it to have substantial organisational effects. Second, the costs of early puberty are much higher for females than males, since the penalties of gestating a child before full adult morphology is reached could be fatal to both mother and offspring. Females, therefore, may be advantaged by carefully adjusting their developmental trajectory based on postnatal experiences, whereas males, who face no such cost, can afford to make earlier 'decisions' regarding the rate of their maturity.

There is a further option that the high testosterone environment causes male foetuses to develop in to more masculine and attractive men, allowing them to enhance their inclusive fitness by maturing and reproducing early with multiple women. This strategy would be advantageous to any man who could successfully operate it. Later developing men in low stress environments be able to gain an advantage by continuing social learning (i.e. childhood) for longer in order to enhance their ability to accrue resources and, thereby, increase their attractiveness as long term partners. The benefits of delayed maturation in terms of social development may, therefore, balance potential costs to attractiveness and masculinity early in life. The experiments within this thesis do not provide sufficient information to decide between these alternatives.

12.1.4 Early development and high dominance: potential costs.

Chapter 10 introduced a possible long-term cost of high dominance; increased cortisol levels. Although cortisol is vital for healthy stress response in humans, prolonged exposure can cause

severe damage to the system, increasing the chances of heart disease and strokes among other health problems. This finding is in line with results from a number of experiments on other, non-human primates where dominant males are often shown to have increased levels of stress hormones, presumably due to the effort of attaining and maintaining a high dominance position, as well as being constantly vigilant to threats to that position. Consequently, high cortisol may represent a cost of high dominance in human males.

Chapter 11 reported an investigation into potential costs of early development, building on ideas from Chapter 6 that early developing men appear to be older than their peers. A technique for the automatic evaluation of skin texture using wavelet analysis is introduced and then used to analyse the skin of early versus late developing men. An intriguing result emerges that the two groups of men do, in fact, differ in their skin texture. However, upon controlling for variation in background luminance, this relationship vanishes. The only resilient effect is with skin luminance, in that later developing men are shown to have lighter skin as adults than earlier developing men. Given that background luminance is being controlled for, this is likely to be due to differences in the reflectivity of the skin, which is related to skin oiliness and sebum production. If earlier developing men are producing less sebum than later developing men then there is a possibility that their skin quality will suffer, since sebum protects the skin from environmental assault, and that they will, as a consequence of extrinsic aging, appear to age faster than later developing men.

12.1.5 Rapid development and hominid evolution: a proposition

The earliest unequivocal emergence of the *Homo* body plan is represented by the 1.5 million year old fossil specimen, KNM-WT15000 (Narikatome boy). The anatomical features of this specimen (classified as either *Homo erectus* or *H. ergaster*) represent a major adaptive shift from previous hominid species in terms of post-cranial anatomy and also brain enlargement and dental anatomy. Hominid species from previous time periods (2.5-1.5 million years ago) were characterised by adaptations towards powerful chewing; large cheek teeth, robust mandibles and crania, and

powerful chewing musculature, the so-called 'robust' morphology (Grine 1989). The emergence of genus *Homo* in the hominid fossil record is associated not only with a steady increase in brain size (as indicated by fossil crania and endocasts), but a more gracile craniodental morphology, as the presumed result of a dietary shift away from coarse, fibrous foodstuffs towards meat-eating (Foley 2002). Intriguingly, the emergence of genus *Homo* is also associated with a slowing of life-history trajectory (as assessed by tooth development and eruption, epiphyseal fusion and calculations based on bone mass (Bermudez de Castro et al. 1999; Foley 2002); Hayton, 2007. pers comm). As previously mentioned, humans have the slowest life history trajectory of all the primates (Sacher 1978), with a particularly extended period of childhood that is, presumably, an adaptation towards learning the complexities of the human social arena. Given that human social complexity is associated with human brain size (Aiello & Dunbar 1993; Dunbar 1995; Dunbar 1998), it is extremely interesting that the increase in brain size within genus *Homo* appears to go hand in hand with a lengthening of life-history phases.

Chapter 6 showed that early developing humans are more facially masculine than later developing males, and it has been a central theme of this thesis that late developers can offset costs to their physical attractiveness with increasing their ability to accrue resources through social learning. It is possible, therefore, that the course of human morphological evolution has been shaped by a necessary slowing of life history trajectory as a result of increasing brain size and social complexity and that as a consequence of the feminising effect of later development, human morphology has become more and more gracile. This hypothesis could be explored by examining links between endocast sizes, the emergence of gracile features and the lengthening of life history in hominids.

If this tentative suggestion is accurate, then there are immediate implications for the future morphology and behaviour of our species, dependent on socioeconomic influences on pubertal timing. Two possibilities present themselves; an increase in the trend for birth rate to decline could encourage an increase in investment in offspring quality and further increases in delayed

maturation, leading to a steady increase in gracility among humans. Alternatively, the widening of the 'wealth gap' between human groups could drive a widening morphological gap, as differences in investment in offspring, leading to differences in pubertal timing between groups, propel groups developing in poorer socioeconomic areas towards increasing masculinity of appearance and behaviour while those in less stressful socioeconomic environments show an increase in femininity.

In the absence of further study, these suggestions remain speculative.

12.2 Future Directions

The proposed, dominance dependent dual male mating strategy is certainly worthy of further study. Predictions can be advanced from the data presented here that high dominance men should differ in their preferences for short term and long term female partners while low dominance men may show a stable partner preference across the two conditions. Furthermore, high dominance men should be expected to engage in more extra-pair copulations when in a long-term relationship than low dominance men. Both of these predictions can be easily tested.

The proposed greater sensitivity of high dominance men to odorous cues of female condition can also be investigated in more depth. Sensitivity could be more accurately determined using different concentrations of the putative pheromones (for example using the 'Sniffing Sticks' experimental protocol (Wolfsenberger 2000)) thus establishing a baseline sensitivity to the compounds for low and high dominance men. This may also reveal more variation in sensitivity to the putative male pheromones. The proposed link between cortisol and pheromonal sensitivity as a mediating factor in the relationship between olfaction and dominance is also worthy of further attention. Inducing stress prior to the exposure to pheromones would be one potential way by which this proposition could be investigated, although short term exposure to cortisol may not be enough to modulate olfactory sensitivity.

The conclusions surrounding the effects of pubertal timing on men will remain speculative until the triggers of male puberty are more clearly understood. Investigations into the effect of post-natal stress on male pubertal timing would be especially useful to the work presented here, given the proposed link between prenatal stress and timing of puberty presented in Chapter 8. Furthermore, results showing links between early life stress, weight gain, socioeconomic status and pubertal timing (Belsky et al. 1991; Moffitt 1993) in human females could be replicated in males, in order to increase the understanding of the process of puberty in men.

The proposed costs of both high dominance (health problems due to cortisol) and early puberty (increase extrinsic ageing due to decreased sebum production) are long-term effects and require long-term study to properly validate. In fact, a longitudinal study of a cohort of males from a variety of socioeconomic backgrounds would be of great use in validating most of the puberty related results in this thesis, as well as providing useful information on the proposed plastic effects of dominance on behavioural and physiological variables by tracking individuals as they move through different social arenas and experience changes in their own social status.

12.3 General Conclusion

This thesis has presented a variety of techniques and methodologies to investigate the effects of pubertal timing (a life history variable) and dominance (a social variable) on the mating tactics, appearance and endocrinology of adult, human males. To some extent, detailed work has been sacrificed for breadth of study, although this process has led to the identification of two new methods of investigation (use of the reorderable list to quantify mate preferences and the use of gabor wavelet analysis to quantify and analyse skin texture) as well as to an array of results showing that both pubertal timing and dominance have relationships with adult male appearance and behaviour. Early puberty has been shown to associate with increased interest in casual sex, increased masculinity and attractiveness and accelerated ageing, all of which were predicted from a life historical approach assuming that early puberty represents investment in reproduction over

continued growth. The fact that pubertal timing may be associated with prenatal hormonal events adds support to the proposition that the life history trajectory of human males is influenced by environmental effects *in utero*. As a contributing factor to male mate value, dominance has been shown to be associated with preferences for mate characteristics and female faces in a manner that suggests the existence of a condition-dependent, dual mating strategy in men. Both puberty and dominance are shown to have hormonal correlates which provide potential mechanisms for the effects they have on male on male appearance and behaviour, including effects, such as accelerated aging or increased stress, which may be counted as associated costs. This thesis provides a useful backing for further study in this area and represents the successful conclusion of an often necessarily exploratory investigation.

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