Early Childbearing and Behavioural Flexibility in the United Kingdom

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Abstract

Work in behavioural ecology has been and continues to be highly informative in the study of human reproductive variation and behavioural flexibility. The traditional focus of this approach has largely been on calibrations in reproductive behaviour in ultimate terms (i.e. a specific behaviour is adaptive and maximizes fitness in different environments). Yet, understanding the ultimate function of human behaviour as adaptive to local environments allows for the deeper study of the proximate psychological, social and physiological mechanisms that can shift both reproductive timing and corresponding reproductive ideals, giving greater insight into the factors that influence early childbearing. Therefore, in the thesis I aim to explore and confirm some of the mechanisms that impact on male and female reproductive timing.

Firstly, I demonstrate that the impacts of social and environmental stressors such as the local sex ratio result in different response patterns from women with different socioeconomic backgrounds, the implication being that women with different life history trajectories have different strategic responses to environmental conditions in line with the predictions of life history theory. Secondly, I show that individuals’ subjective perceptions of their environment are just as important, and potentially more important, indicators of their fertility intentions than the often used objective indicators of environment quality such as deprivation. Thirdly, I show that individuals take risks in strategic ways that can be explained by evolutionary principles and that their future reproductive intentions are supported by pro-natal norms and are not due to deficiencies in their knowledge of safe sexual practice. Fourthly, I consider the evidence that kin networks help shape individuals’ psychology around life history strategies. Finally, I explore the causal pathways by which acute stress shifts individuals’ life history strategies and how this adjustment is moderated by an individual’s exposure to chronic childhood stressors.
The findings resulting from this work merges with other research in the field of behavioural ecology, moving towards an integrated understanding of human reproductive and behavioural calibrations and exploring the ultimate and proximate questions of human reproductive variation. These findings highlight the importance of understanding life history trade-offs as central to reproductive scheduling. In addition it provides policy makers and health workers with an alternative way of understanding early childbearing, one that sees human behaviour within its adaptive evolutionary context.
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Declaration

Whilst registered as a candidate for the above degree, I have not been registered for any other research award. The results and conclusions embodied in this thesis are the work of the named candidate and have not been submitted for any other academic award.

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Dissemination of Research

Chapter 2

Chapter 3

Chapter 4
Chapter 1

General Introduction

1.1 Overview

As the factors that predict and calibrate human childbearing and sexual behaviours are often complex and multifaceted it is unsurprising that there are several different theoretical approaches to the study of human reproductive behaviour. Psychology and the social sciences have largely looked at the human example in isolation from other species, focusing on questions such as how women decide when to begin childbearing (Arai, 2003), how early childbearing adjusts women’s affective states (Thompson, 1986) and how young motherhood impacts on social and economic inclusion (Kidger, 2004). On the other hand, behavioural ecologists’ investigation of human behaviour is informed by comparative evidence and understanding human behaviour in its adaptive evolutionary context (Dickins, Johns, & Chipman, 2012). Despite some hostility towards an evolutionary approach from some authors (Nelkin, 2000; Hagen, 2005) and common misconceptions that an evolutionary approach promotes genetic pre-determinism and de-emphasizes social context, a behavioural ecological approach is not in conflict with the social sciences (see Nettle, 2009 for a discussion). The conclusions drawn from an evolutionary approach are often closely aligned to those of the social sciences. Evolutionary biologists and social scientists working without reference to evolutionary theory often arrive at remarkably similar conclusions.
regarding the factors influencing reproductive variations (Geronimus, Bound, & Waidmann, 1999; Low, Hazel, Parker, & Welch, 2008).

One of the strongest arguments for a behavioural ecological approach to the study of human reproduction is that there is a wealth of comparative evidence from other species and well-developed theory concerning the factors likely to affect reproductive timing. These can assist in the understanding of human reproductive flexibility as being imbedded within a specific ecological and evolutionary context. At the centre of behavioural ecology, however, lies a black box approach to understanding variation in reproductive timing, often referred to as the phenotypic gambit (Grafen, 1984). Essentially, while there is assumed to be a connection between behaviour and the mechanisms that influence the behaviour of interest, allowing researchers to study behavioural strategies in ultimate terms (e.g. the fitness benefits of calibrating reproductive timing), the proximate mechanisms are not measured directly. Thus behavioural variation is explained using the concept of phenotypic plasticity, which assumes that the same genotype can give rise to multiple phenotypes depending on ecological conditions. In other words, adjustments in reproductive timing can be viewed as adaptive behavioural calibrations with the ultimate goal of maximizing individuals' reproductive success under particular environmental conditions (Sear, Lawson, & Dickins, 2007). Equally important to the understanding of individual variation in the timing of reproduction is the study of the proximate mechanisms that link the ecological conditions to behavioural responses as the ultimate adaptive function of human behaviour is only half the picture.

The objective of this thesis is to contribute to the attempts begun by researchers approaching human behavioural sciences from an evolutionary perspective to integrate ultimate and proximate explanations of behavioural flexibility (Nettle, 2011). This thesis therefore asks both ecological questions about ultimate causes (i.e. how is variation in reproductive timing adaptive to environmental conditions), and psychological questions about mechanisms that influence behavioural adaptations (i.e. what is the role of intrasexual
competition, subjective perspectives of environmental quality, etc.) and begins to unify the answers.

The approach will also be multi-methodological. Most research into human reproductive variation is by nature correlational. There is a strong tradition of research that explores differentiated female reproductive timing and its antecedents using large data sets (Quilan, 2003; Pesonen et al., 2008; Low et al., 2008). In a similar vein, researchers commonly utilise surveys and self-report questionnaires to look at how psychological and social mechanisms relate to an individual’s stated fertility intentions (Nettle & Cockerill, 2010; Chipman & Morrison, In Press). Likewise, this thesis aims initially to follow in the footsteps of the majority of human behavioural ecology research into reproductive variation by looking at how demographic variables of small areas predict variations in fertility scheduling (Chipman & Morrison, 2013) before looking at how psychological mechanisms influence adolescents’ fertility intentions (Chipman & Morrison, In Press); however, the aim of this thesis, for various reasons is also to branch out from the familiar methodological approaches to the study of human reproductive variation. In the first place, the heavy reliance on self-reported data by means of questionnaires and surveys, which is now the dominant method of investigation in human behavioural sciences (Baumeister, Vohs, & Funder 2007; Furr 2009), is potentially a cause for concern. While, work by Nettle, Coall and Dickins (2011) has demonstrated that at the onset of adulthood (age 16) individuals have formed conscious intentions regarding their ideal timing of parenthood, there is always the possibility that individuals’ actual behaviour may be substantially different from their claims about it, especially if social judgements are attached to certain patterns of behaviour. This leads to problematic questions about the reliability of self-reported data (Garro, 2010). In order to create a fuller account of human reproductive variation, this thesis will expand out of these approaches to studying human behaviour and attempt to look more closely at how individuals’ experiences of stress might be an underlying proximate mechanism behind these psychological mechanisms and
demographic predictors of early age of first birth and to explore through experimental manipulation the causal effects of acute stress on an individual’s stated fertility intentions.

Additionally, correlational research may miss important patterns in day to day interactions and individual behaviours that are only apparent through the direct observation of the specific behaviours of interest. Therefore an ethological approach will also be used to confirm and extend understanding of how behaviour changes adaptively. In short, research will be conducted via large data sets, surveys and questionnaires, experiments and ethological approaches to create a holistic understanding of human reproductive variation with particular emphases placed on the evolutionary context and how individuals respond adaptively to local conditions in order to maximise their reproductive success.

In the first chapter, biological explanations of reproductive variation and comparative evidence are considered before addressing how this theory and evidence informs the study of human reproductive variation and early childbearing. Next, the social sciences’ explanations for early fertility are presented, and criticisms of an evolutionary perspective are put forward and responded to. Finally, political perspectives and media representations of early reproduction are considered before a closer look is taken at reproductive variation in the United Kingdom.

In chapter 2, I explore how the operational sex ratio of a small geographic area predicts the birth rate of the population. Previous studies have shown that the local sex ratio can affect mate market dynamics in human populations (Griskevicius, Tybur, Ackerman, Delton, Robertson & White, 2012); here we show that the local sex ratio also has an impact on female fertility schedules where female-biased sex ratios are associated with higher birth rates. This affects women from different positions on the socioeconomic gradient in a manner consistent with the principles of the life history theory. This finding both strengthens the notion that the scarcer sex becomes in demand, and has the greater influence on subsequent behaviour (female-bias potentially increasing female intrasexual competition and
favouring male mating preferences). Furthermore, these patterns also suggest that female-female competition encourages poorer women to adopt a fast life history strategy and give birth early, and richer women to adopt a slow life history strategy and delay reproduction.

In chapter 3, I explore the psychological mechanisms that predict fertility intentions exploring how kin networks, mating and reproductive risk taking, discount preference, and perceptions of environmental risk predict individual differences in fertility preferences in a socioeconomically diverse sample of adolescents. Importantly, this research indicates that individuals’ subjective life expectancies and perceptions of their environment better predicted fertility intentions than did structural measures of environmental quality. This suggests that by the time individuals reach adolescence they are monitoring the mortality risk and the conditions of their local environments and are adjusting their temporal outlook and decisions about the relative trade-offs of current versus future reproduction. Levels of grandparental investment also predicted parenting preferences, suggesting that cooperative breeding may play a role in reproductive decision making. There was also evidence that patterns of risk taking behaviours could be adaptive to environmental conditions and some evidence that pro-natal attitudes, as opposed to knowledge of safe sexual practice, predict adolescents’ reproductive strategies. These findings suggest that studying individuals’ domain-specific psychological mechanisms from a life history perspective adds to our understanding of the persistently high rates of early reproduction within developed countries such as the United Kingdom.

In chapter 4, I propose that acute stress has the potential to influence an individual’s reproductive ideals and that the way an individual responds to stress depends on their adaptive life history strategies shaped by their exposure to chronic stressors. Accumulated evidence suggests that a chronic exposure to stress is associated with an earlier age of reproduction in humans. The majority of this research, however, is correlational, and does not prove that high stress causes an accelerated onset of female reproductive ideals.
Therefore, in order to explore the causal links between stress and reproductive variation I used an experimental paradigm designed to activate both the autonomic nervous system and the hypothalamic-pituitary-adrenal axis and examined the effect of acute stress on females’ reported reproductive ideals. My findings indicate that acute stress calibrates individuals’ fertility intentions. Furthermore, individuals who reported more exposure to early childhood stress responded to the acute stress condition by reporting earlier reproductive ideals. Excitingly, these findings offer the first experimental evidence that stress can alter women’s reproductive decision making.

In chapter 5, I use an ethological approach to confirm and extend our understanding of how behaviour changes based on the supply of the opposite sex were found in both animal and human populations. To do this I observed male and female behaviour and looked for evidence of competition based on the sex ratio of the immediate vicinity in a public, natural setting as part of two explorative pilot studies. Results were mixed and one pilot study did not account for potential pseudo-replication of the data. Despite the serious limitations of both pilot studies, understanding how intrasexual competition influences and predicts sexual signalling is a crucial step in completing our understanding of how the operational sex ratio (OSR) is linked both to human mating preferences and human fertility scheduling. There is also considerable scope to add to the understanding of male and female sex differences in sexual signalling if such a study is done correctly.

In chapter 6, I summarize my findings and discuss their implications in terms of creating a fuller account of understanding human reproductive calibrations as adaptive domain-specific response to conditions of a local environment. I also highlight some limitations of my research and discuss how future studies could complement and build on the results presented in the course of this thesis.

The findings resulting from this thesis constitute a multi-methodological account of human reproductive variation and behavioural flexibility in the United Kingdom. This thesis also adds
to the understanding of how behaviour is evolutionarily adaptive and attempts to synthesize this ultimate explanation of reproductive variation with an understanding of the causative proximate mechanisms at work calibrating the phenotypic expressions of human behaviour. This research, therefore, has the potential to not only be important in exploring an alternative to traditional policy and health care initiatives in dealing with societal issues such as teenage pregnancy in areas that are persistently at risk, and in improving the life situations of adolescents and adolescent parents, but also as it puts forward how a broad evolutionary approach as outlined by Tinbergen (1963) is invaluable for exploring and addressing issues in the human behavioural sciences.

1.2 Biological explanations of reproductive variation and comparative evidence

In behavioural biology, variation in fertility schedules is understood to arise from the fitness benefits of key reproductive trade-offs. The central tenet of the evolutionary biology model of animal behaviour is inclusive fitness. Inclusive fitness (hereafter fitness) is the sum of direct (reproduction) and indirect (investment in the offspring of relatives) fitness.

An often-used heuristic utility in evolutionary ecology regarding trade-offs made by species is referred to in terms of $r$ and $K$ selection (MacArthur & Wilson, 1967; Pianka, 1970). In an ecological equation, $r$ refers to the growth rate of a population, while $K$ indicates the carrying capacity of the environment in which that population exists. Thus, in unpredictable environments, individuals are $r$-selected, which leads to faster maturation, smaller growth, earlier and more frequent reproduction and wide dispersal of offspring. $r$-selected organisms are unlikely to gain fitness benefits from entering into competition with others due to the changeability of the environment and they tend to colonize ecological niches that are not overly crowded, that is to say such populations are a considerable distance from the carrying
capacity of the local environment. The best strategy for these organisms is to grow fast, reproduce often and have their young disperse. On the other hand, in stable, predictable environments, $K$-selected organisms compete for access to resources and invest in specializations to exploit their local environment. As a consequence the population size of $K$-selected individuals is often near to the carrying capacity of the ecology. Such individuals mature slowly, requiring much parental effort, grow larger, live longer and reproduce at a lower frequency than $r$-selected individuals.

This model is not a binary ‘all or nothing’ in terms of $r/K$ selection; most often it is viewed more as a continuum, with most species falling somewhere between total $r$-selection and total $K$-selection. This makes sense as, for example, any organism within a predominantly $r$-selected ecology would gain some fitness advantage from developing even the smallest specializations that gave it a competitive edge. As a consequence such traits would reach fixation and shift the species towards the $K$ end of the continuum. Thus organisms develop evolutionarily stable strategies that position them somewhere on an $r/K$ continuum.

$r/K$ selection, however, is not without its critics (Stearns, 1977). As a measure of population growth, $r$ is critically dependent on population density and environmental uncertainty and is also a true measure of fitness in that it refers directly to reproduction. $K$, on the other hand, is no such measure, but rather a composite of a population, its resources and the interaction of the two. In short, the concepts of $r$ and $K$ may not be logically equivalent and cannot be mounted on a continuum. Therefore, organisms are more commonly referred to as being distributed on a fast to slow life history continuum, as the tenets of the life history theory capture the dynamics of fitness maximizing as a system of trade-offs across the whole of the lifespan of an organism.

One crucial trade-off for organisms is between the quantity and the quality of the offspring they produce. On one hand, producing a large number of offspring would be favoured by natural selection when there are limited resources or the quality of the local environment is
poor, with extrinsic mortality argued to be the key driver of environment quality (Hill, 1993).
Under such ecological circumstances an organism should have a large number of offspring which will result in the organism not being able to invest heavily in each offspring. This strategy should increase the chances of fitness gains for the organism since, due to the sheer volume of reproduction, some offspring will survive and reproduce even though some of the offspring may not survive due to underinvestment. In contrast, in a predictable environment with plenty of resources, leaning towards greater parental investment in fewer offspring in order to increase offspring quality should lead to better fitness gains. Such high quality offspring are more likely to be reproductively successful adults and will be better prepared to deal with harsh conditions and future uncertainty. Gustafsson, Qvarnström, & Sheldon (1995) found that the brood size of collared flycatchers was inversely related to the development of secondary sexual characteristics in male offspring resulting in consequences for the male’s reproductive potential, as males with large patches mate with more females and have higher lifetime reproductive success. This work is an example of the trade-off between offspring quality and quantity, as smaller broods better equipped with sexual ornamentation and thus higher quality compared with offspring from larger broods.

Another key trade-off that species face is between diverting resources from somatic maintenance to reproductive effort. Ecological variables predict an evolutionarily stable balance point for this trade-off. On the one hand, an unpredictable environment might lead to earlier reproductive effort and thus fewer resources being invested in somatic growth and maintenance. Alternatively, a stable environment might lead to greater somatic investment as building and maintaining a more robust body will potentially increase longevity and as a result increase reproductive potential. However, under conditions of ecological stress, developing a large body will become more difficult to achieve and its energetic expense may reduce fitness opportunities relative to individuals who grow quicker and reproduce sooner. In other words, investing more time and energy in growth increases the chance of an organism dying before reproduction in risky environments. This set of relationships can be
captured as a trade-off between current versus future reproduction, which has only three outcomes: no current reproduction, some resource allocation to the present and some to the future, or total current reproduction followed by death (Kaplan & Gangestad, 2005).

Take, for example, the case of the Trinidadian guppy *Poecilia reticulata* where fecundity is directly proportional to the size of the guppies. In a series of experiments Reznick (1983) demonstrated that non-reproducing females stored significantly more energy in fat tissues as opposed to investing energy in somatic growth while for reproducing guppies increases in the amount of energy invested in reproduction were matched by decreases in the energy devoted to somatic tissues.

Furthermore, in a series of fascinating field experiments, Reznick and Endler (1982) demonstrated that differences in guppy life histories were associated with differences in the predation risks. Guppies from streams where fish preyed primarily on larger guppies matured earlier, had greater reproductive efforts and produced more and smaller offspring than did guppies from locations where fish tended to prey on small, immature guppies, thus providing rather neat evidence that extrinsic mortality is associated with the development of an organism’s life history strategies and that organisms can adapt their life history trajectory in order to maximize their reproductive potential. Reznick and Endler went even further; by transplanting the fish they changed their life history strategies and traits in only a few generations. This example of behavioural phenotypic flexibility also adds the concept of within species life history variations to the idea of between species distribution on the fast to slow life history continuum. As with the population level and species level differences in life history strategies, within a species individual organisms should be expected to calibrate strategies and adopt different life history trajectories in response to local ecological conditions in order to maximize fitness (Chisholm, 1993; Ellis, 2004).
1.3 Human reproductive variation and early childbearing

When the ideas of the life history theory are applied to humans a compelling argument is made that, relative to the overall population in which they live, certain individuals adopt fast life history strategies characterized by early sexual maturation (Belsky, Steinberg, & Draper, 1991) and investment in early reproduction (Chisholm, 1993) as such individuals reproduce well before the population mean in Western democracies (Kramer & Lancaster, 2010). These individuals can therefore be seen as opting for current rather than future reproduction.

Perhaps the first researchers to apply these principles to human behavioural flexibility and calibrated reproductive strategies were Draper and Harpending (1982). In their paper they argued that early experiences help form lifelong patterns in an individual, in other words the individual’s life history strategy. The chief focus of their paper was on the effects of father absence in children, noting that girls in father absent families were more likely to go on to be promiscuous in their teenage years and were also less likely to develop good long-term relationships as adults. In contrast, girls raised in father present households were more likely to delay sexual behaviour and long term relationships were maintained more successfully.

Draper and Harpending came to the conclusion that the primary difference between these girls’ life history trajectories was that in the case of the child brought up in a father absent family the individual has little or no expectation of paternal investment whilst the other trajectory expects significant paternal investment in offspring. These two differing behavioural strategies serve to maximise fitness under the conditions in which they were developed. In short, the authors argued that a child’s experience of paternal investment during development is key to helping individuals form judgements about the local reproductive ecology as well as the potential strategies of future mates.

The principles of this analysis were extended by Belsky et al. (1991) in their seminal paper in which they made the case that father absence is just one aspect of early socialization that can impact upon an individual’s future life history strategy. The authors focused on how
these strategies would maximise the fitness of an individual and emphasized the adaptive nature of individual strategic behavioural flexibility, pointing out that as in non-human species humans will have been selected to be flexible to environmental conditions within certain parameters. Thus, according to Belsky et al., early life experiences of the predictability and availability of resources and interpersonal relationships, which they termed contextual stress, would impact on the development of reproductive effort. An individual experiencing poor interpersonal relationships and limited resources should begin reproduction at younger ages and invest in parenting less, compared to those with more positive early life experiences. What the authors predicted and for which they provided some supporting evidence was that contextual stressors would induce early puberty and as a result sexual maturation. That is, environmental conditions cue a suite of physiological and behavioural changes, such as early menarche, in an individual that will affect their reproductive and parental investment strategies, and girls who experience chronic stress during development will mature faster and begin reproduction sooner, and do so without great paternal investment.

Since the publication of Belsky et al. (1991) there has been a great deal of research and work demonstrating the relationship between chronic early life stressors and accelerated puberty and teenage pregnancy (Belsky, Houts, & Fearon, 2010; Belsky, Steinberg, Houts, & Halpern-Felsher, 2010; Bogaert, 2008; Chisholm, Quinlivan, Peterson, & Coall, 2005; Ellis & Garber, 2000; Ellis, McFadyen-Ketchum, Dodge, Pettit, & Bates, 1999; Gaudie et al., 2010; Moffitt, Caspi, Belsky, & Silva, 1992). These findings add support to the theory based on life history principles that in order to maximize reproductive potential and adapt to environmental conditions, women in harsh and unpredictable environments characterized by high rates of mortality and low income should favour early reproduction in order to complete their reproductive careers before the risk of dying or becoming incapacitated becomes too great. On the other hand, women in low mortality, high income environments should postpone the onset of reproduction. Through delaying childbearing they give themselves an extended
period to invest in their own development and resource accumulation that may then be used to produce higher quality offspring (Chipman & Morrison, 2013). Thus women adopt suites of behaviours consistent with either a fast or slow life history strategy; towards the fast end of a continuum, favouring earlier reproduction and towards the slow end of the continuum, favouring delayed reproduction.

These findings perhaps help create a sensible theory that explains the relationship between economic deprivation and teenage pregnancy that are commonly cited in the social science literature (Arai, 2009) — a relationship that is at the core of governmental and policy concerns as will be discussed in more detail later. One feature that an evolutionary perspective adds to the study of reproductive variation in humans which is invaluable is not simply the ability to demonstrate a relationship between several key variables and accelerated reproductive timing, but also a life history interpretation of behavioural and reproductive flexibility which allows for the development of testable predictions regarding differences, both in actual behaviour and intentions between early and later reproducing mothers.

While selection should favour a point where the costs and benefits of reproductive trade-offs are optimized, life history theory treats calibrations in reproductive behaviour in ultimate terms (i.e. a specific behaviour is adaptive and maximizes fitness in different environmental conditions). Therefore, it can only make predictions about the links between particular ecologies and behavioural responses. An equally important approach is the study of the proximate mechanisms that connect specific ecologies with behavioural responses, a process that has been begun by behavioural ecologists, although this approach is often more of a goal than a reality at present (Sear, Lawson, & Dickins, 2007; Nettle, 2011).
1.4 The social sciences and criticisms of an evolutionary perspective

The relationship between ecological conditions associated with fast life history strategies (i.e. harsh and unpredictable environments) and teenage pregnancy is commonly cited in the social science literature (Arai, 2009), yet the emphasis is often not on adaptive behavioural and reproductive strategies young people employ in response to poor ecological conditions but on adolescents' risk taking, sensation seeking and inadequate sex education leading to unwanted pregnancies (Donohew, et al., 2000; Kirby, 2001; Saito, 1998). When early pregnancy is seen as a pragmatic strategy it is seen as a form of benefits cheating, a means of securing housing and income for the young mother (Dickens, Johns & Chipman, 2012). This is problematic as it perpetuates the counter-intuitive notion that teenage pregnancy prevention policies will act to reduce poverty and social exclusion rather than acknowledging that the situations women are living in contribute to the timing of reproduction (Geronimus, 1991, 1992). This account also ignores the fact that girls from deprived areas who are most likely to conceive at younger ages are much less likely to have an abortion than girls from wealthier backgrounds (Lee, Clements, Ingham, & Stone, 2004). This suggests that these pregnancies are not in fact unwanted but that individuals are making the decision (either consciously or subconsciously) to start reproducing in light of their present conditions and assumed future stability.

The discrepancy between how the social sciences explain reproductive behaviour and evolutionary explanations may, in part, be due to the social sciences' traditional focus on the developmental or proximate causes of young birth and have often ignored the ultimate causes of early reproduction. While a broad evolutionary approach as outlined by Tinbergen (1963) looks at questions relating to the function and evolution of behaviour in addition to the mechanics and development of an organisms behaviour. In some quarters there is also a degree of antipathy towards biologically based explanations of human behaviour (Nelkin, 2000) which are often seen to imply genetic pre-determinism. Critiques of the value of such
explanations are reactive to earlier racial and hereditarian thought, claiming that social organisation and behavioural differences between human societies and groups are a result of social transmission, not heredity (Boas, 1940). However, researchers working from an evolutionary perspective are not implying that different patterns of behaviour are a consequence of inter-group genetic differences but rather of the environmentally induced phenotypic plasticity of behaviour (Laland & Brown, 2011).

Hostility to biological explanations of behaviour has also stemmed from a different understanding of the definition of what constitutes a biological explanation. Social scientists have characterized biological explanations of behaviour as concerned only with physiological and cognitive processes within the individual, ignoring or failing to capture the socially determined and developmental dimension of human behaviour (for an example see Durkheim, 1992). On the one hand, social factors must be turned into patterns of thought and cognition and on a proximate physiological level, neural signals, if they are to influence behaviour (Nettle, 2009). On the other hand, it is also an inaccurate depiction of the concept of biological explanations to suggest that they are limited to the physiological and cognitive process occurring in a single individual. No biological explanation of behaviour could possibly be complete if it was limited to individual processes without considering environmental ones.

Studies of primates, for example, demonstrate how the reproductive success of these organisms depends on their complex and intricate social structures (see Dunbar, 1996, for example). In the human case, there is evidence that societal differences in paternal investment are adaptive based on the difference fathers can make to offspring outcomes (Kaplan et al., 1998; Nettle, 2008). As discussed previously, father absence can play a large role in calibrating an individual’s life history trajectory and ultimately their reproductive success within environmental constraints. These social factors that influence behavioural
variation are thus evolved, domain-specific mechanisms that respond adaptively to ecological conditions and produce an appropriate behavioural response.

Merely to assert that people’s reproductive ideals are socially constructed and thus differ across societies does not say anything about why the pattern of behaviour in populations where there are high rates of mortality and low income should favour early reproduction (Low et al., 2008). Nor does it say anything about why within societal differences can reflect patterns similar to the differences between societies, for example where individuals from low socioeconomic positions in the United Kingdom have younger ages of first birth than other members of society (Nettle, 2009). Not only is an evolutionary explanation of behavioural variation often the most parsimonious but also its position within a Darwinian framework allows for the development of testable predictions. For example, evolutionary theory would predict that adolescents with different fertility ideals should have different perspectives of environmental quality and their risk of their own mortality (see chapter 3). Indeed, difference in individuals’ perception may well impact upon temporal outlook (Chisholm, 1999a) affecting decisions about the relative trade-offs of current versus future reproduction.

There is, however, another form of human cultural behaviour which displays itself in ways different from the pattern of environmental plasticity. This domain includes the person to person transmission of behaviours and thought which are learnt from the social group. The numerous and distinctive cultures and traditions among human societies are ample evidence of the importance of transmitted culture in the formation of human societal organisation and between population differences. An evolutionary framework predicts that social learning will appear where the environment is somewhat stable and the costs of individual learning to reproductive success are high. Mathematical models of social evolution have demonstrated that when individual and social learning is in balance and individual learning is always optimal for reproductive success it is most likely that the population is also assisting an individual to maximize their fitness (McElreath & Boyd, 2007). In other words, an
evolutionary theory of social learning would predict that individuals use social learning to maximise fitness given their environmental constraints. There are two kinds of social learning that should predict variation in reproductive timing. The first involves individuals’ observation of their social environment. Research on young mothers found that they were aware of how the health of other women in their immediate neighbourhoods and social groups had changed over time and they directly related this to their own reproductive goals and likelihood of completing their reproductive careers before the cost of morbidity and mortality became too great (Geronimus, 1996). It could be argued that this is just a form of environmental plasticity, as a domain-specific mechanism is responding adaptively to ecological conditions to produce an appropriate behavioural response. However, there is also a second type of social learning that involves directly copying the reproductive behaviour of others. There is evidence that girls’ reproductive timing closely follows that of their mothers in most Western populations including the United Kingdom (Meade, Kershaw, & Ickovics, 2008; Nettle et al., 2011). Evolutionary theory predicts that this generational transmission should be favoured for behaviours which affect fertility, and for which the environment (in this case the family unit) is stable across generations (McElreath & Strimling, 2008).

1.5 Political perspectives and media representations of early reproduction

Governments work with populations and economies. Thus they are primarily concerned with the potential risks to health and well-being associated with teenage pregnancy, namely: teenage mothers are less likely to complete their education; are more likely to be poor, have higher rates of postnatal depression and higher rates of infant mortality compared with mothers who delay parenthood (Paranjothy, Broughton, Adappa, & Fone, 2009). Therefore, media headlines and government policy perpetuate the assumption that early conception is the result of an individual’s mistake caused by a limited understanding of sexual education or
a lack of skills related to contraceptive use. Individuals who have children at young ages are portrayed as risk takers, or ‘savvy benefit cheats’, as the argument of the tabloid and broadsheet press is often that women with fast life history trajectories from economically deprived backgrounds become teenage mothers in order to increase their opportunities for receiving child and housing benefits (see Dickins et al., 2012, for a discussion).

On the other hand, elevated propensity towards risk taking is also most common during adolescence (Steinberg, 2007) and risky sexual behaviour and conduct related behavioural problems suggest a relatively risk prone profile for young mothers. It is, therefore, not surprising that the main thrust of governmental policy for the last decade has been focused on increasing access to contraception and sex education for girls from poor socioeconomic backgrounds (Teenage Pregnancy Strategy Evaluation, 2005). Yet despite the millions of pounds spent on lowering the national rate of teenage pregnancy in England and Wales (Paton, 2002), the under-18 conception rates remain persistently high in the most at risk communities.

If, however, young people are acting in a risky manner, it is also possible that their risk taking behaviours are rational responses to their disadvantaged backgrounds. In the same way that an individual's life history trajectory may involve a trade-off between reproductive effort now and parenting effort in the future (Gangestad & Simpson, 2000), individuals who perceive the future as dangerous may be more willing to take a higher number of risks for immediate rewards rather than adopt a more conservative approach and wait for delayed rewards when there is such an uncertain return.

It remains an open question how sophisticated the thought process is that goes into setting up reproductive goals and to what extent reproductive timing (particularly early childbearing) is consciously planned. It is not clear, however, that the assumption is justified that young people who conceive are taking excessive risks or lack a proper understanding of sexual practice. Qualitative researchers (Duncan, 2007; Arai, 2003; Cater & Coleman, 2006) have
been struck by how elaborately young women can reason about their life situations. In many ways their reasoning and arguments, an exchange between the costs and benefits of current and future childbearing, relate rather neatly to the life history theory model as relating to reproductive variation. For example, teenagers and young women appreciate that early fertility will impact their chances of investing in their own development (education, career, etc.). At the same time they are also able to articulate that due to poor environmental conditions and other adversities they are concerned about how long they will remain in good somatic health, and thus want to be able to complete their reproductive careers before the threat of morbidity and mortality become too great. In short, it appears that individuals do weigh up their current condition and future prospects and the outcome of their assessment drives their motivation for early reproduction (Cater & Coleman, 2006; Seamark, 2001; Harden, Brunton, Fletcher, & Oakley, 2009).

1.6 Reproductive variation in the United Kingdom

There is a great deal of variation in women’s age of first birth across socioeconomic gradients in Western societies, such as the United Kingdom. The United Kingdom is an extremely unequal society and extrinsic risks and threats to life expectancy are surprisingly high in particular areas (Marmot, 2010) and, as an evolutionary perspective would predict, an uneven pattern of teenage conception rates emerges for the United Kingdom, historically the highest in Western Europe (Bradley-Stevenson & Mumford, 2007; Westall, 1997). In England, women from the most deprived neighbourhoods give birth on average 8 years before their peers from the least deprived areas (Nettle, 2010). The English national rate of teenage pregnancy was 38.3 per 1000 women aged 15–17 in 2009, and these figures are considerably higher in many of the urban, industrial centres (Armitage, 1997).
Furthermore, girls from deprived areas who do conceive are much less likely to have an abortion than girls from wealthier backgrounds (Lee et al., 2004). For example, in Winchester the teenage conception rate was 18.3 per 1000 women aged 15–17 in 2009, of which 51.3% went on to have an abortion, while in Gosport, a more deprived area of Hampshire, the teenage conception rate for 2009 stood at 31.3, with 33.8% of those leading to an abortion (ONS, 2013). The lower rates of abortion among girls from poor backgrounds suggest that they are making an active fertility decision to become teenage mothers. It has been argued (Arai, 2003) that for the less affluent groups having a baby brings some sense of purpose and associated status gains, whereas for wealthier girls a pregnancy puts educational and career opportunities at risk. It would seem that the latter group are future oriented, and the former significantly discount their future and maximize more immediate gains.

While politicians, the media and social scientists all acknowledge and understand that deprivation is linked to local teenage pregnancy rates they often ignore the fact that many young women may be choosing to have children while they are still in good health (Geronimus, 1996). Attempts to reduce teenage pregnancy rates through targeting proximate economic, educational or health correlates are unlikely to be as successful as a strategy that is devised from understanding the importance of life history trade-offs as central to reproductive scheduling. Such methods are more likely not only to succeed but also to have a lasting effect on reversing the rate of teenage pregnancy in areas that are persistently at risk and, importantly, on improving the life situations of adolescents and adolescent parents.
Chapter 2

The impact of sex ratio and economic status on local birth rates

2.1 Overview

Human mating and reproductive behaviour can vary depending on various mechanisms including the local sex ratio. Previous research shows that as sex ratios become female-biased, women from economically deprived areas are less likely to delay reproductive opportunities to wait for a high-investing mate but instead begin their reproductive careers sooner. Here, I show that the local sex ratio also has an impact on female fertility schedules. At young ages, a female-biased ratio is associated with higher birth rates in the poorest areas, whereas the opposite is true for the richest areas. At older ages, a female-biased ratio is associated with higher birth rates in the richest, but not the poorest areas. These patterns suggest that female-female competition encourages poorer women to adopt a fast life history strategy and give birth early, and richer women to adopt a slow life history strategy and delay reproduction.
2.2 Introduction

Humans exhibit considerable within species variation in reproductive behaviour. One well established finding is that high mortality, harsh environments favour early reproduction (Nettle, 2011). Yet research on many species has demonstrated that the operational sex ratio (OSR) affects the relative importance of reproductive behaviours, such as mate choice and sexual competition, which can have a knock-on effect to actual fertility scheduling. OSR is the ratio of sexually active males to sexually receptive females (Kvarnemo & Ahnesjö, 1996), and in both animal and human populations the scarcer sex becomes in demand and has the greater influence on subsequent behaviour (Jirotkul, 1999; Pedersen, 1991).

In humans, male-biased populations have been associated with higher crime rates, perhaps indicating increased male-male competition (Hudson & Den Boer, 2002). Furthermore, where there is a male-biased ratio, women’s mate preferences become more selective, resulting in the limited marital success of low socioeconomic status men (Pollet & Nettle, 2008). In contrast, societies with female-biased ratios favour male mating preferences. For example, across cultures female-biased populations tend to have higher marital instability as demonstrated by increased divorce rates and lower remarriage rates (Trent & South, 1989). In addition, female-biased OSRs increase non-marital reproduction amongst females living in deprived areas as they fail to attract high-investing spouses and begin to reproduce at younger ages (Staples, 1985). There is also evidence that a female-biased ratio lowers women’s expectations of the opposite sex. This has been shown experimentally where women’s expectations of the amount of money men will spend on them when dating is lowered when there are fewer men available (Griskevicius et al., 2012).

In this study, I aim to shift the discussion from mate market dynamics to fertility scheduling by examining the effect of OSRs on birth rates between neighbourhoods in England. Birth rates can serve as another important indicator of intrasexual competition as females may adjust their reproductive timing based on the relative number of potential mates in their local
environment. Furthermore, women’s responses to female-biased OSRs are likely to differ based on their socioeconomic status and position on the life history continuum.

Women of high socioeconomic status with slow life history characteristics may respond to environmental stressors by moving further towards the slow end of the life history continuum and delaying reproduction. This is supported by experimental research which has already demonstrated that slow life history strategist are more likely to shift further towards their end of the continuum when faced with risk and uncertainty (Griskevicius, Tybur, Delton, & Robertson, 2011). Conversely, low socioeconomic status women with fast life history strategies may seek to have children sooner in response to the same environmental conditions. Therefore, low socioeconomic status women in female-biased neighbourhoods may begin reproducing earlier in a bid to maximize their fitness by strategically adopting fast life history characteristics rather than delaying reproduction in the hope of attracting a high-investing mate and investing in offspring quality. I predict that (i) in the most deprived United Kingdom neighbourhoods, birth rates at young ages will be higher when the OSR is female-biased; (ii) in the least deprived neighbourhoods, birth rates at older ages will be higher when the OSR is female-biased.

2.3 Method and Materials

My research focused on England, where economic inequality is high relative to other developed nations and material conditions between neighbourhoods can vary markedly within the space of a few kilometres, particularly in urban areas. I conducted my analysis at ward level, as wards are the primary unit of British administrative geography and the smallest area of geography for which the Office for National Statistics (ONS) releases data on birth rates.
There are a total of 7933 Census Area Statistical wards in England, which were used for the 2001 census outputs. As wards can vary in both geographical and population size I retained 5223 urban wards for analysis. I focused on urban wards because in rural areas wards can be sparsely populated which might result in less intrasexual competition. Furthermore, due to greater distances, individuals must travel in rural areas to reach their workplaces or to socialize with friends and family and they may be more mobile, leaving their local area more frequently. Hence the sex ratio that affects their behaviour may not be a feature of the ward itself. Wards are defined as urban if they belong to a metropolitan area whose population is greater than 10,000 (mean population = 7984, SD = 4342) (ONS, 2004).

Data on live births by ward and mothers’ age were released as the rate of live births per 1000 female population in aggregate three year bands (ONS, 2011). Data were taken for the years 2005–2007 and mothers’ ages were aggregated into quintiles from 15–19 years to 35–39 years. Strict password protection arrangements prevented individuals being identified. Wards with fewer than five conceptions were suppressed to further protect individuals from identification, leaving 2876 wards for my study.

I calculated the OSR for each ward as the ratio of males to females between 15 and 50 years of age living in a particular ward (Lummaa, Merilä, & Kausse, 1998). OSRs greater than one indicate a male bias. Population figures were taken from the Mid Year Population Estimate released by the Office of National Statistics for 2007 (mean = 1.00, SD = 0.84) (ONS, 2012). The range for OSRs in the most deprived 50% of urban wards was 0.74–1.71 (SD = 0.97), and in the least deprived 50% of urban wards was 0.68–1.79 (SD = 1.10). These figures included individuals normally resident in a ward, including prisoners, boarding school students and armed forces personnel, meaning that some wards with small populations were heavily male biased (OSRs >1.4). Exclusion of these wards from the analysis did not alter the statistical significance of the approach.
Chapter 2

Sex ratio and economic status

To measure ward level deprivation, I used the Index of Multiple Deprivation (IMD) for 2007 (ONS, 2007). The IMD is a composite index of socioeconomic hardship that includes income, employment, health, education, housing and access to services. Higher scores indicate more deprived areas. Scores ranged from 1.44 to 79.18 (mean = 23.80, SD = 13.83).

Using R (2012) I created generalized linear models fitted by the Laplace approximation (Bolker et al., 2008) with OSR, IMD and age as fixed variables and birth rate as the response variable, treated as a proportion and analysed with a generalized linear model. I ran individual models for live births at each age category to determine the direction of effects of OSR, IMD and their interaction at separate birth rate quintiles.

2.4 Results

Up to the age of 29, increased deprivation was associated with a higher birth rate, whereas after age 29, decreased deprivation was associated with a higher birth rate. These results suggest that poorer women gave birth at younger ages, whereas wealthier women delayed reproduction until they were older. In general, female-biased OSRs were associated with higher birth rates, although for two out of five age categories this effect was not significant. The interaction between OSR and IMD was significant at each age category except for ages 25–29. Under age 25, female-biased OSRs were associated with higher birth rates in deprived areas, but lower birth rates in less deprived areas. After age 29, this pattern reversed, and female-biased OSRs were associated with higher birth rates in less deprived areas, and lower birth rates in more deprived areas (see Table 2.1), supporting both predictions.
Table 2.1 Parameter estimates with effect sizes for birth rate by age quintile. Data presented from five generalized linear models.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>p</th>
<th>Partial η²</th>
</tr>
</thead>
<tbody>
<tr>
<td>15-19 Birth Rate</td>
<td>Intercept</td>
<td>-4.879</td>
<td>0.083</td>
<td>&lt;.001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>OSR</td>
<td>-0.069</td>
<td>0.083</td>
<td>ns</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>IMD</td>
<td>0.038</td>
<td>0.002</td>
<td>&lt;.001</td>
<td>0.018</td>
</tr>
<tr>
<td></td>
<td>OSR * IMD</td>
<td>-0.006</td>
<td>0.002</td>
<td>&lt;.05</td>
<td>0.006</td>
</tr>
<tr>
<td>20-24 Birth Rate</td>
<td>Intercept</td>
<td>-3.257</td>
<td>0.049</td>
<td>&lt;.001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>OSR</td>
<td>-0.179</td>
<td>0.049</td>
<td>&lt;.001</td>
<td>0.011</td>
</tr>
<tr>
<td></td>
<td>IMD</td>
<td>0.034</td>
<td>0.002</td>
<td>&lt;.001</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>OSR * IMD</td>
<td>-0.020</td>
<td>0.002</td>
<td>&lt;.001</td>
<td>0.000</td>
</tr>
<tr>
<td>25-29 Birth Rate</td>
<td>Intercept</td>
<td>-2.388</td>
<td>0.043</td>
<td>&lt;.001</td>
<td></td>
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<tr>
<td></td>
<td>OSR</td>
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<td>0.043</td>
<td>&lt;.001</td>
<td>0.028</td>
</tr>
<tr>
<td></td>
<td>IMD</td>
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<td>0.002</td>
<td>&lt;.01</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>OSR * IMD</td>
<td>-0.002</td>
<td>0.002</td>
<td>ns</td>
<td>0.009</td>
</tr>
<tr>
<td>30-34 Birth Rate</td>
<td>Intercept</td>
<td>-2.226</td>
<td>0.042</td>
<td>&lt;.001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>OSR</td>
<td>-0.438</td>
<td>0.042</td>
<td>&lt;.001</td>
<td>0.014</td>
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<tr>
<td></td>
<td>IMD</td>
<td>-0.024</td>
<td>0.002</td>
<td>&lt;.001</td>
<td>0.018</td>
</tr>
<tr>
<td></td>
<td>OSR * IMD</td>
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<td>0.002</td>
<td>&lt;.001</td>
<td>0.013</td>
</tr>
<tr>
<td>35-39 Birth Rate</td>
<td>Intercept</td>
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<td>0.054</td>
<td>&lt;.001</td>
<td></td>
</tr>
<tr>
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<td>OSR</td>
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<td>0.053</td>
<td>ns</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>IMD</td>
<td>-0.027</td>
<td>0.002</td>
<td>&lt;.001</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>OSR * IMD</td>
<td>0.018</td>
<td>0.002</td>
<td>&lt;.001</td>
<td>0.001</td>
</tr>
</tbody>
</table>

To display the shift in the direction of the interaction effect after age 25 the regression line for birth rates by age quintile is plotted against OSR for socioeconomic status terciles in Figure 2.1.
Figure 2.1 Birth rates plotted against OSR. Logistic regression lines are presented for each socioeconomic status tercile, and the data points have been removed for clarity. Significant interactions are marked with an asterisk.

2.5 Discussion

I show that in addition to the well-established effect of deprivation, OSR also predicts the birth rate. Furthermore, female-biased OSRs predict early reproduction in the most deprived wards. This effect reverses at older ages, such that from age 30 it is in the least deprived wards where female-biased OSRs predict higher birth rates. Each variable only explained a small amount of the variance in overall birth rate, but this is not surprising given that the
Chapter 2

Sex ratio and economic status

decision to have children is complex, with many different factors contributing to birth rates (Hardy, Astone, Brooks-Gunn, Shapiro, & Miller, 1998). Furthermore, the effect size of OSR is at similar levels to effects of deprivation which is a well-established antecedent of age of first birth. These findings are consistent with Pedersen's (1991) prediction that individuals will adjust their behaviour as a result of same sex competition induced by differences in the sex ratio. My interpretation of the findings is that as the chance of attracting a high-investing partner is reduced in female-biased wards, perhaps due to increased female-female competition, women from deprived areas calibrate towards the fast end of the life history continuum. Thus they begin to reproduce earlier, boosting early reproduction in these areas. By contrast, women from less deprived areas with slow life history characteristics adopt the opposite strategies in response to female-biased OSRs and delay reproduction (Griskevicius et al., 2011). I suggest, therefore, that the interaction between ward level deprivation and OSR is vital to understanding individual adjustments to fertility schedules. Given the geographical scale of wards, I must consider the psychological and biological reality of such neighbourhood divisions. Previous research has highlighted the importance that subjective experiences of local neighbourhoods play in predicting teenage pregnancy, even compared with environmental predictors such as ward IMD (Johns, 2011). Wards are local ecologies which individuals can monitor for perceived environmental risks and perhaps the supply of one sex to the other which may be related to reproductive behaviour, accounting for my results. Wards might be an especially salient factor for those from the low end of the socioeconomic gradient due to lower geographical mobility, as reduced car ownership and greater unemployment may mean individuals are less likely to travel beyond their local neighbourhoods, making the environment of their ward particularly important.

To my knowledge, this is the first time that the effect of the OSR on human birth rates has been shown in a national sample in a developed country at the level of small geographical areas, that is, wards. This study adds to the growing evidence that the ratio of sexually active and competing males to females explains various aspects of male and female
behaviour. In principle, this study demonstrates that an oversupply of females within a local economically deprived environment leads young women to adjust their strategies for reproductive success by beginning their reproductive careers earlier and thus predicts an increase in the rate of teenage pregnancy within that environment.
Chapter 3

Fertility and parenting ideals in urban adolescents

3.1 Overview

Previous research on contemporary childbearing has identified a strong relationship between environmental conditions such as economic deprivation and early fertility. Less is known, however, about the social-psychological mechanisms that mediate these environmental predictors of early fertility at the individual level, and the extent to which they are consistent with life history theory. The aim of this research is to determine how kin networks, mating and reproductive risk taking, discount preference and perceptions of environmental risk predict individual differences in fertility preferences in a socioeconomically diverse sample of adolescents. Questionnaires were administered to 333 adolescents (245 female) between the ages of 13 and 19 years, attending schools in urban neighbourhoods in Hampshire, United Kingdom. Individuals’ subjective life expectancy and perception of their environment better predicted fertility intentions than did structural measures of environmental quality. This suggests that by the time individuals reach adolescence they are monitoring the morbidity and mortality risk of their environment and are adjusting their reproductive ideals accordingly. Levels of
grandparental investment also predicted parenting preferences, suggesting cooperative breeding may play a role in reproductive decision making. There was also evidence that patterns of risk taking behaviours could be adaptive to environmental conditions and some evidence that pro-natal attitudes, as opposed to knowledge of safe sexual practice, predict adolescents’ reproductive strategies. These findings suggest that studying individuals’ psychology from a life history perspective adds to my understanding of the persistently high rates of early reproduction within developed countries, such as the United Kingdom.

3.2 Introduction

There is great variation in the age of first birth (AFB) across socioeconomic gradients in Western societies. An uneven pattern of distribution emerges for teenage conception rates in the United Kingdom, historically the highest in Western Europe (Bradley-Stevenson & Mumford, 2007; Westall, 1997). In England, women from the most deprived neighbourhoods give birth on average 8 years before their peers from the least deprived areas (Nettle, 2010). The English national rates of teenage pregnancy were 38.3 per 1000 women aged 15–17 in 2009, and these figures are considerably higher in many of the urban, industrial centres (Armitage, 1997).

The relationship between poor socioeconomic circumstances and the increased likelihood of conceiving while a teenager suggests the importance of environmental cues in the occurrence of teenage parenthood. For instance, Wilson and Daly (1997) report a positive correlation between homicide rates and teenage pregnancy in deprived neighbourhoods in Chicago and suggest that individuals calibrate reproductive schedules towards early childbearing based on the high extrinsic mortality rates in the surrounding area. This is in line with the principles of life history theory, whereby organisms attempt to maximize fitness through a series of reproductive
Fertility and parenting ideals

trade-offs (Nettle, 2011). These trade-offs can be dynamic and respond adaptively to the ecological conditions of the individual. In areas of high mortality, for example, organisms tend to favor early sexual maturity and current over future reproduction as the least risky strategy to ensure sufficient time and opportunity to mate and produce offspring before the probability of death becomes too high. When applied to humans and teenage mothers a compelling argument is made that, relative to the overall population in which they live, certain individuals adopt fast life history strategies characterized by early sexual maturation (Belsky, Steinberg, & Draper, 1991) and investment in early reproduction (Chisholm, 1993). This is brought on by poor socioeconomic conditions, high rates of extrinsic mortality, and other indices of environmental harshness and unpredictability.

Research on geographical variations in teenage pregnancy and AFB has been useful in assessing neighbourhood effects and the impact of material conditions on fertility outcomes; however, structural neighbourhood characteristics are only a small part of the picture. It has been argued that research simply linking indices of deprivation to local teenage pregnancy rates can miss the possibility that a minority of the female population are influenced in their reproductive motivation at the individual level, and does not examine the nature of the psychological mechanisms that trigger their behavior (McCulloch, 2001). One further question therefore, concerns whether or not an individual’s attitudes towards their environment is associated with their reproductive motivation. In a recent study, Johns (2011) demonstrated that women’s perceptions of environmental risk are a better predictor of teenage motherhood in a United Kingdom population than structural indicators of material deprivation. Johns argued that such perceptions may affect the individual’s temporal outlook (see also Chisholm, 1999a or b), affecting decisions about the relative trade-offs of current versus future investments. Individual variations in the perception of mortality and environmental risk may influence reproductive motivation in adolescents. Furthermore, there is evidence that perceived social support and
social cohesion can play an important role in shaping positive health outcomes. Perceptions of positive (support) and negative (risk to self) neighbourhood factors are potentially of equal importance when an individual is making judgements about when to begin to reproduction. These life strategies and attitudes would then be adaptive to specific ecological conditions. Essentially, early reproduction may be a rational (though not necessarily conscious) response to perceived external environmental uncertainty in terms of high perceived risk and low perceived support.

Another strong predictor of an earlier AFB is the level of investment received during childhood and young adolescence. Girls whose fathers were absent or uninvolved in their development reach menarche earlier than average (Alvergne, Faurie, & Raymond, 2008; Bogaert, 2008; Ellis, 2004), have sexual intercourse younger (Quinlan, 2003), and are more likely than average to become mothers at a young age (Chisholm, Burbank, Coall, & Gemmiti, 2005; Ellis et al., 2003; Hogan & Kitagawa, 1985). Not being breastfed and separated from the mother in childhood also predicted earlier AFB (Nettle, Coall, & Dickins, 2011). In addition to the robust effect of parental investment, the presence of close, intact grandparental and kin networks may also act as a prenatal cue. One argument for this potential association is that individuals with close kin networks are embedded in cooperative breeding networks enabling them to begin childbearing at younger ages as they are better able to manage motherhood due to the close familial support (Sear & Dickins, 2010). The most common support for teenage mothers comes from their own mothers, and it may be that these soon-to-be-grandparents are also responsible for provisioning for and investing in offspring, thereby increasing their fitness. Furthermore, Coall and Hertwig (2011) noted that grandparental investment may be especially beneficial under conditions of socioeconomic duress where childrearing support and expertise is particularly useful in lieu of the necessary financial means to provide non-kin childcare and other services. However, there is an argument that close intact kin networks might have the opposite effect and serve to delay
reproduction. Large kin networks may also increase the competition between relatives, as has been shown to occur in viscous populations, who disperse slowly from their environment at birth (Taylor, 1992). This creates a certain paradox as the close kin networks that may promote cooperative breeding efforts may instead lead to resource competition between kin that undermines any such benefits. Furthermore, strong kin networks, as indicated by multiple generations of surviving relatives, may also be a signal of low mortality environments associated with later age of first birth.

While evolutionary based theories of cooperative breeding and life history theory treat early childbearing as a rational attempt at improving reproductive success, teenage motherhood is often regarded by policy makers as a consequence of risky sexual behavior or substandard sexual education and therefore unrelated to rational planning. Risk taking is common during adolescence (Steinberg, 2007); it is, therefore, not surprising that the main thrust of governmental policy for the last decade has been focused on increasing access to contraception and sex education for girls from poor socioeconomic backgrounds (Teenage Pregnancy Strategy Evaluation, 2005). Yet despite the millions of pounds spent on lowering the national rate of teenage pregnancy in England and Wales (Paton, 2002), the under-18 conception rates remain persistently high in the most at risk communities. An evolutionary approach would explain this variance in risk-taking propensity by suggesting that such behavior may be adaptive in certain environments (Daly & Wilson, 2001). Belsky et al. (1991) suggested that the level of parental care experienced during childhood may affect adult mating strategies. Low parental responsiveness to their child’s needs, which are generally cued by harsh environments, may lead individuals to adopt short-term mating strategies which are better suited to unpredictable ecologies where long-term bonds are not needed or anticipated. In addition, there may also be differences between male and female adolescents due to sex differences in potential reproductive rates (Clutton-Brock & Parker, 1992) with men potentially competing more
for mating opportunities.

The objective of this study was to compare these different perspectives at the individual level and see how attitudes to teenage pregnancy relate to kin networks, perception of risk, propensity towards risk taking behavior and knowledge of safe sexual practice (KSSP). This will help resolve whether early reproduction is a rational strategy as outlined above, or the result of irrational or careless behavior and limited sex education. The geographical focus of this study is on urban south Hampshire, an area that has in the past been supported by large port-based industries and has now suffered decline and economic hardship. This includes the unitary authorities of Portsmouth and Southampton and the non-metropolitan districts of Gosport and Havant and covers a socioeconomically mixed area where deprivation and the rate of teenage pregnancy vary considerably. By sampling a cross section of adolescents from different backgrounds in Hampshire, this study hoped to explore the extent to which each of the four domains mentioned influence differences in reproductive intentions.

3.3 Methods

3.3.1 Participants

A total of 333 adolescents (245 female) between the ages of 13 and 19 years were recruited either when they visited the University of Portsmouth for a university Open Day or through approaching local schools in Hampshire. The number of students and the age range varied from school to school, depending on factors which were random with respect to the study, such as school timetables and demands of the teachers, and participants from each school were drawn from a broad spectrum of socioeconomic backgrounds. Participants were asked to give their gender, age, and socioeconomic status measured by father’s occupation. Individuals who did
not know their father’s occupation answered unknown. Occupations were then classified on a 5 point scale from higher managerial, administrative and professional occupations (1) to routine occupations and unemployed (5) following the Standard Occupational Classification developed by the Office of National Statistics (ONS, 2010). It should be noted that it is unusual to include males in a study of reproductive scheduling and fertility intentions (for an exception see Kim, Smith and Palermiti, 1997). However, as there is new evidence to suggest there are few differences in ideal reproductive intentions between males and females (Nettle & Cockerill, 2010), my measure allowed for both sexes to be studied and I looked at the responses of both. The majority of the sample (86%) was white British.

The population of Hampshire in 2010 was estimated to be 1,731,700 of which 286,165 were 18 years and younger (ONS, 2011). Urban areas make up 83% of the population in Hampshire and account for 100% of the most deprived areas locally, as measured by the Index of Multiple Deprivation, a composite index of socioeconomic hardship that includes income, employment, health, education, housing and access to services. These urban areas, however, are fairly heterogeneous and also host some of the least deprived areas in Hampshire. Just over half of all urban areas in Hampshire can be found in the 20% and 40% least deprived quintiles nationally (Joint Strategic Needs Assessment, 2008). As with deprivation, rates of teenage pregnancy also vary widely between areas in Hampshire, with the highest rates concentrated around the pockets of high deprivation. For example, the rate of teenage births in Portsmouth and Southampton (port cities on the south coast of England) were 50 and 49.2 per 1000 women compared with 28.9 per 1000 women in the rest of the county (Botting, Rosato, & Wood, 1998).
3.3.2 Measures

All participants completed an anonymous survey on their own, either online or on paper. There were two outcome variables, including free text response to the questions; “At what age do you want to have your first baby?” and “What would be the ideal number of children you want to have?” Stated fertility intentions were used as a proxy measure of actual reproductive scheduling based on Nettle et al. (2011), who showed that, at the onset of adulthood (age 16), individuals have formed conscious intentions regarding their ideal timing of parenthood. Furthermore, the responses given were strong predictors of their actual ages of conception and childbearing even when the event occurred years later. I was interested in the number of children females reported wanting, not only as another measure of fertility intentions, but also due to the current debate in the UK about cutting child benefits. The government’s assertion is that individuals should adjust their family size according to income and the implicit assumption is that families from the lowest end of the socioeconomic gradient are having too many children (Dickins, Johns, & Chipman, 2012).

3.3.2.1 Personal networks

Participants were asked how close they feel to parents and grandparents, how often they see each other, and how comfortable they are talking about matters that are important to them or asking for help. Responses were rated on a bipolar scale from strongly agree (2) to strongly disagree (-2). Negative scores indicated less contact and investment from parents and grandparents. There were five questions on each of the parental and grandparental scale (see Appendix A). The sum total of participants’ responses were recorded. The numerical range on the parental investment scale and on the grandparental investment scale was from -10 to 10.
Participants checked a box to indicate if they were no longer living with one or both of their biological parents and were given blank scores on this measure (n=40).

### 3.3.2.2 Environmental risk

To measure perceptions of their immediate environment’s harshness and uncertainty, participants were asked both about their local neighbourhood (described as their street or building block) and about their school or college environment; as my participants spend a large portion of time in their educational environment. The perceptions of environmental and school risk measures were designed for this study, modifying questions from existing sources that have attempted to evaluate individual perceptions of neighbourhood risk (Moore & Chase-Lansdale, 2001; Siahpush et al., 2006; Steptoe & Feldman, 2001). Participants answered questions that dealt with ambient hazards as well as their perceptions of social cohesion of their residential and school environments. This included questions on how honest, trustworthy, and interested in helping they perceived others to be in each environment, as well as how safe they feel (i.e. I feel safe walking alone at night, for neighborhood perceptions; I worry about being the target of bullies, for school perceptions) (See Appendix A). The environmental risk scale contained 5 items (numerical range -10 to 14) and the school risk scale 7 items (numerical range -14 to 14). Responses were rated on a bipolar scale (strongly agree = 2, strongly disagree = -2) with negative scores indicating greater perceived environmental risk.

Subjective life expectancy (SLE) was measured based on the measure devised by Hill, Ross, & Low (1997). Participants were asked, “How likely is it that you will be alive at these ages?” Eight age categories were listed (20–29, 30–39, 40–49, 50–59, 60–69, 70–79, 80–89, and ≥90 years), with blanks to fill in the estimated likelihood (ranged from 0 to 100%) of being alive in each of
the eight age categories. An example was given to illustrate how to fill in the blanks.

As a structural indicator of the environmental quality of the local area, I included the measure of Index of Multiple Deprivation (IMD) (ONS, 2007) for the catchment area of each school as a predictor of adolescents’ fertility intentions. Higher scores indicate more deprived areas.

We also looked at the teenage pregnancy rate of the local unitary authority or non-metropolitan district of the school as a structural indicator of early fertility in the local area. This rate is calculated as the number of conceptions per 1,000 women aged 15–17 resident in the area using the mid-year population estimates. Data were taken for the years 2005–2007 and were compiled by the Office of National Statistics (ONS, 2010).

### 3.3.2.3 Risk taking behaviour

Perceptions of risk and uncertainty included a measure of discount preference developed by Chesson et al., (2006). This measure indicates a willingness to forego immediate gratification for future gratification and is thus a proxy for risk taking. Discount rates were calculated based on participants’ responses to three hypothetical questions about the possible payoff of a prize. In the first question, the participants were asked if they would prefer a prize of £400 today versus a prize of £1,200 a year from today. In the second and third questions, the future prize was reduced to £800 and £500, respectively. From their responses, individuals were categorized from those who strongly favoured delayed gratification (1) to those who strongly favoured immediate gratification (6).

In addition to the influence of life history trade-offs on risk taking, the current paradigm in behavioural decision making research acknowledges that risk taking is domain-specific and that
individuals show variation in risk propensity and the likelihood of engaging in that type of behavior across different domains. Kruger, Wang, & Wilke, (2007) developed a measure that identified five evolutionary domains of risk taking, including mating and reproduction.

Scores on mating, reproductive, and total risk taking were taken from the Evolutionary Domain-Specific Risk Taking scale (see Wang, Kruger, & Wilke (2009) for the measure used, taken from Kruger et al. (2007)). All participants responded to a set of questions on mating and reproductive risk, and rated each question in terms of the likelihood of engaging in perceived riskiness of the stated risky behavior on a bipolar scale (very unlikely/ not at all risky = -2 and very likely/very risky = 2). The mating risk scale assessed an individual’s attitudes towards risky sexual behaviors such as engaging in one night stands while the reproductive risk scale assessed an individual’s attitude towards taking risk that might impact on their ability to have children such as exposing themselves to chemicals that might lead to infertility. Higher scores indicated a higher likelihood of engaging in the risky activity and lower perceived riskiness (numerical range -6 to 6).

3.3.2.4 Knowledge of safe sexual practice

In addition, the survey collected data on the students' KSSP. These questions were classed as either objective KSSP or subjective KSSP. Objective questions were based on factual knowledge and could be answered either True or False (e.g. “If a condom breaks, there is a pill you can take afterwards to prevent pregnancy”, “Teens need their parents’ permission to buy birth control, not including condoms”. Higher scores indicated greater factual knowledge of safe sexual practice. Subjective questions required answers based on the participant’s opinion (e.g. “Condoms are too much trouble to use”, “It is unhealthy for girls to use birth control”). Possible responses ranged from strongly agree (1) to strongly disagree (5). Higher scores indicate
stronger pro-natal, anti-contraceptive attitudes. There was no significant correlation between the measures of objective and subjective KSSP.

3.3.3 Analytic strategy

To study the relationship between personal networks, perceptions of environmental risk, risk taking behaviour and knowledge of safe sexual practice, I used a General Linear Mixed Models (GLMM), created in SPSS Version 20. Participants were entered in the model as the level 1 units, and schools as the level 2 units within which participants were nested. A model was considered a significant improvement over a simpler model based on the change in the Akaike Information Criterion (AIC) (Kuha, 2004). I first built a base model with just socioeconomic status (SES) and sex as level one predictors, before adding the level one predictors which include variables in the domains of personal networks, environmental risk, risk taking propensity and finally KSSP. As I had both male and female participants, I also added the interaction effect of the participants’ sex on their fertility intentions. Significant effects were only considered if the model with additional predictors was more informative than the base model. Multi-collinearity between variables was assessed to determine their appropriateness in the final model. There were no serious correlations between independent level 1 variables or the school level variables, and the variance inflation factor was found to be acceptable for all variables (VIF <1.5) (Miles & Shevlin, 2001). For the final model, I presented parameter estimates alongside the standard error and p value for the predictors which were significant or approaching significance.

This study was approved by the Ethics Committee of the University of Portsmouth and carried out with the agreement of all participating schools. Participants completed the survey during
class time and were free to omit responses or to refrain from submitting their questionnaire. Participants crossed a check box to indicate that they understood the nature of the survey and that it would be used in a research study. In order to keep participation and responses anonymous, no individual identifying personal information was collected.

3.4 Results

Table 3.1 shows the descriptive statistics for the predictor and outcome variables.
### Table 3.1 Descriptive statistics for the main predictor and outcome variables

<table>
<thead>
<tr>
<th>Variable</th>
<th>Range</th>
<th>Mean (SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perceived neighbourhood risk*</td>
<td>(-10 to 10)</td>
<td>1.51 (3.62)</td>
</tr>
<tr>
<td>Perceived school risk*</td>
<td>(-14 to 14)</td>
<td>4.34 (3.29)</td>
</tr>
<tr>
<td>Subjective life expectancy (years)</td>
<td>(23 to 89)</td>
<td>66.62 (12.17)</td>
</tr>
<tr>
<td>Index of Multiple Deprivation ** (school level variable)</td>
<td>(3.32 to 26.83)</td>
<td>10.79 (4.01)</td>
</tr>
<tr>
<td>Teenage pregnancy rate (school level variable)</td>
<td>(5 to 94)</td>
<td>28.23 (18.79)</td>
</tr>
<tr>
<td>Parental investment ***</td>
<td>(-6 to 10)</td>
<td>3.47 (2.54)</td>
</tr>
<tr>
<td>Grandparental investment ***</td>
<td>(-6 to 10)</td>
<td>4.77 (3.07)</td>
</tr>
<tr>
<td>Mating risk taking (likelihood) ♦</td>
<td>(-6 to 6)</td>
<td>-2.02 (2.62)</td>
</tr>
<tr>
<td>Mating risk taking (perceived riskiness) ♦</td>
<td>(-6 to 6)</td>
<td>1.22 (2.12)</td>
</tr>
<tr>
<td>Reproductive risk taking (likelihood) ♦</td>
<td>(-6 to 6)</td>
<td>-3.58 (2.50)</td>
</tr>
<tr>
<td>Reproductive risk taking (perceived riskiness) ♦</td>
<td>(-6 to 6)</td>
<td>2.84 (2.53)</td>
</tr>
<tr>
<td>Discount preference °</td>
<td>(1 to 6)</td>
<td>2.46 (1.02)</td>
</tr>
<tr>
<td>Objective knowledge of safe sexual practice ¬</td>
<td>(-9 to 9)</td>
<td>6.60 (2.44)</td>
</tr>
<tr>
<td>Subjective knowledge of safe sexual practice ±</td>
<td>(-12 to 12)</td>
<td>3.49 (3.21)</td>
</tr>
<tr>
<td>Ideal age of first birth (years)</td>
<td>(18-36)</td>
<td>26.81 (3.07)</td>
</tr>
<tr>
<td>Ideal number of children</td>
<td>(0-10)</td>
<td>2.59 (1.15)</td>
</tr>
</tbody>
</table>

* High scores indicate less perceived environmental risk  
** High scores indicate more deprivation  
*** High scores indicate more investment  
♦ High scores indicated a higher likelihood of engaging in the risky activity and lower perceived riskiness  
° High scores indicate desire for immediate rewards  
¬ High scores indicated greater factual knowledge of safe sexual practice  
± High scores indicate stronger pro-natal, anti-contraceptive attitudes.
Age of first birth (AFB) was predicted by both adolescents’ perceptions of neighbourhood risk ($B = 0.30$, SE = 0.12, $p = .01$) and their perceptions of school risk ($B = -0.17$, SE = 0.07, $p = .01$) (see Table 3.2).
Table 3.2 Parameter estimates for ideal age of first birth from the generalized linear mixed model

<table>
<thead>
<tr>
<th>Parameter estimate</th>
<th>SE</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>23.66</td>
<td>2.32</td>
</tr>
<tr>
<td>Sex</td>
<td>-0.38</td>
<td>2.11</td>
</tr>
<tr>
<td>Perceived environmental risk</td>
<td>0.30</td>
<td>0.12</td>
</tr>
<tr>
<td>Perceived school risk</td>
<td>-0.17</td>
<td>0.07</td>
</tr>
<tr>
<td>Subjective life expectancy</td>
<td>0.06</td>
<td>0.02</td>
</tr>
<tr>
<td>Socioeconomic status (father's income)</td>
<td>0.13</td>
<td>0.21</td>
</tr>
<tr>
<td>Index of Multiple Deprivation</td>
<td>-0.04</td>
<td>0.06</td>
</tr>
<tr>
<td>Teenage pregnancy rate</td>
<td>-0.06</td>
<td>0.03</td>
</tr>
<tr>
<td>Grandparental investment</td>
<td>0.33</td>
<td>0.19</td>
</tr>
<tr>
<td>Parental investment</td>
<td>0.08</td>
<td>0.09</td>
</tr>
<tr>
<td>Discount preference</td>
<td>-0.89</td>
<td>0.53</td>
</tr>
<tr>
<td>Mating risk taking (Likelihood)</td>
<td>-0.14</td>
<td>0.09</td>
</tr>
<tr>
<td>Mating risk taking (perceived riskiness)</td>
<td>-0.06</td>
<td>0.11</td>
</tr>
<tr>
<td>Reproductive risk taking (likelihood)</td>
<td>0.19</td>
<td>0.09</td>
</tr>
<tr>
<td>Reproductive risk taking (perceived riskiness)</td>
<td>0.06</td>
<td>0.09</td>
</tr>
<tr>
<td>Subjective knowledge of safe sexual practice</td>
<td>-0.21</td>
<td>0.13</td>
</tr>
<tr>
<td>Objective knowledge of safe sexual practice</td>
<td>0.39</td>
<td>0.21</td>
</tr>
<tr>
<td>Sex * Perceived environmental risk</td>
<td>-0.20</td>
<td>0.14</td>
</tr>
<tr>
<td>Sex * Teenage pregnancy rate</td>
<td>0.07</td>
<td>0.03</td>
</tr>
<tr>
<td>Sex * Grandparental investment</td>
<td>-0.47</td>
<td>0.20</td>
</tr>
<tr>
<td>Sex * Discount preference</td>
<td>1.20</td>
<td>0.57</td>
</tr>
<tr>
<td>Sex * Subjective KSSP</td>
<td>0.39</td>
<td>0.16</td>
</tr>
<tr>
<td>Sex * Objective KSSP</td>
<td>-0.36</td>
<td>0.23</td>
</tr>
<tr>
<td>Sex * SES</td>
<td>-0.57</td>
<td>0.25</td>
</tr>
</tbody>
</table>

School was included as a random factor (estimated variance component = 7.76, SD = 0.82)
3.4.1 Environmental Risk and AFB

Interestingly, higher perceived neighbourhood risk decreased adolescents AFB while higher perceived school risk increased ideal AFB. Adolescents who reported shorter subjective life expectancies, also predicted earlier ideal AFBs ($B = 0.06$, $SE = 0.02$, $p < .01$). Of the objective indicators of environmental quality, the IMD did not significantly predict AFB nor did the SES (as measured by father’s income) of the individual adolescent. There was, however, a significant interaction for sex × SES ($B = -0.57$, $SE = 0.25$, $p = .02$) which was stronger for female adolescents. The local teenage pregnancy rate also significantly predicted AFB ($B = -0.06$, $SE = 0.03$, $p = .01$). Adolescents reported earlier ideal AFBs as the rate of under-18 pregnancy rose.

3.4.2 Other Main Effects and AFB

The adolescents’ propensity towards taking reproductive risks also significantly predicted AFB ($B = 0.19$, $SE = 0.09$, $p = .04$). Participants who were less likely to take reproductive risks reported later ideal AFBs. Grandparental investment ($B = 0.33$, $SE = 0.19$, $p = .08$), objective KSSP ($B = 0.39$, $SE = 0.21$, $p = .07$) and discount preference ($B = -0.89$, $SE = 0.53$, $p = .09$) were also trending towards significant associations with ideal AFB. Less grandparental investment marginally predicted earlier AFB, as did less factual knowledge of safe sexual practice. The propensity to discount the future marginally predicted ideal AFB.

3.4.3 Interaction Effects and AFB

There was a significant sex × grandparental investment interaction ($B = -0.47$, $SE = 0.20$, $p = .02$) with the association between grandparental investment and AFB stronger for female adolescents. Interactions between sex and the teenage pregnancy rate ($B = 0.07$, $SE = 0.03$, $p$
=.01), sex and discount preference (B = 1.20, SE = 0.50, p = .04) (see Figure 3.1) and sex and subjective KSSP (B = 0.69, SE = 0.16, p = .01), were all significant with the association stronger for male participants.

**Figure 3.1** Interaction of mean age of first birth (95% confidence intervals) and discount preference by gender
3.4.4 Environmental Risk and Desired Number of Offspring

The lower the participants’ perceptions of neighbourhood (B = 0.05, SE = 0.02, p = .05) and of school risk (B = 0.12, SE = 0.05, p = .02) the greater their desired number of offspring (see Table 3.3).
Table 3.3 Parameter estimates for desired number of offspring from the generalized linear mixed model

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.31</td>
<td>1.28</td>
<td>ns</td>
</tr>
<tr>
<td>Sex</td>
<td>2.66</td>
<td>1.37</td>
<td>.05</td>
</tr>
<tr>
<td>Perceived environmental risk</td>
<td>0.05</td>
<td>0.02</td>
<td>.05</td>
</tr>
<tr>
<td>Perceived school risk</td>
<td>0.12</td>
<td>0.05</td>
<td>.02</td>
</tr>
<tr>
<td>Subjective life expectancy</td>
<td>0.02</td>
<td>0.01</td>
<td>ns</td>
</tr>
<tr>
<td>Socioeconomic status</td>
<td>0.07</td>
<td>0.04</td>
<td>.08</td>
</tr>
<tr>
<td>(father’s income)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Index of Multiple Deprivation</td>
<td>0.01</td>
<td>0.02</td>
<td>ns</td>
</tr>
<tr>
<td>Teenage pregnancy rate</td>
<td>0.00</td>
<td>0.00</td>
<td>ns</td>
</tr>
<tr>
<td>Grandparental investment</td>
<td>0.07</td>
<td>0.03</td>
<td>.00</td>
</tr>
<tr>
<td>Parental investment</td>
<td>0.08</td>
<td>0.05</td>
<td>ns</td>
</tr>
<tr>
<td>Discount preference</td>
<td>-0.16</td>
<td>0.07</td>
<td>.03</td>
</tr>
<tr>
<td>Mating risk taking (likelihood)</td>
<td>0.02</td>
<td>0.03</td>
<td>ns</td>
</tr>
<tr>
<td>Mating risk taking (perceived riskiness)</td>
<td>-0.07</td>
<td>0.04</td>
<td>.05</td>
</tr>
<tr>
<td>Reproductive risk taking (likelihood)</td>
<td>-0.08</td>
<td>0.03</td>
<td>.01</td>
</tr>
<tr>
<td>Reproductive risk taking (perceived riskiness)</td>
<td>0.14</td>
<td>0.05</td>
<td>&lt;.01</td>
</tr>
<tr>
<td>Subjective knowledge of safe sexual practice</td>
<td>-0.06</td>
<td>0.03</td>
<td>.02</td>
</tr>
<tr>
<td>Objective knowledge of safe sexual practice</td>
<td>-0.10</td>
<td>0.07</td>
<td>ns</td>
</tr>
<tr>
<td>Sex * Perceived school risk</td>
<td>-0.12</td>
<td>0.06</td>
<td>.03</td>
</tr>
<tr>
<td>Sex * Subjective life expectancy</td>
<td>-0.03</td>
<td>0.02</td>
<td>.07</td>
</tr>
<tr>
<td>Sex * Parental investment</td>
<td>-0.12</td>
<td>0.06</td>
<td>.07</td>
</tr>
<tr>
<td>Sex * Objective KSSP</td>
<td>0.13</td>
<td>0.08</td>
<td>ns</td>
</tr>
<tr>
<td>Sex * Reproductive risk taking (perceived riskiness)</td>
<td>-0.15</td>
<td>0.06</td>
<td>.01</td>
</tr>
</tbody>
</table>

School was included as a random factor (estimate variance component = 0.90, SD = 0.10)
### 3.4.5 Other Main Effects and Desired Number of Offspring

Higher levels of grandparental investment \((B = 0.07, SE = 0.03, p < .01)\) and a propensity to discount the future \((B = -0.16, SE = 0.07, p = .03)\) also predicted a greater number of desired offspring amongst participants. Lower scores of the subjective KSSP measure predicted a greater number of desired offspring \((B = -0.06, SE = 0.03, p = .02)\). Furthermore, participants who perceived items on the mating risk taking scale as more risky wanted more offspring \((B = -0.07, SE = 0.04, p = .05)\). Participants also reported that they were less likely to take reproductive risks \((B = -0.08, SE = 0.03, p = .01)\) while at the same time perceiving items on the reproductive risk scale to be more risky \((B = 0.14, SE = 0.05, p < .01)\) when they reported a greater number of desired offspring. Lower SES was marginally significant as a predictor of desired number of offspring \((B = 0.07, SE = 0.04, p = .08)\). Sex was also a significant predictor of wanting more offspring with females reporting a desire for more offspring \((B = 2.66, SE = 1.37, p = .05)\).

### 3.4.6 Interaction Effects and Desired Number of Offspring

The interactions between sex and perceptions of school risk \((B = -0.12, SE = 0.06, p = .03)\), sex and subjective life expectancy \((B = -0.03, SE = 0.02, p = .07)\), sex and parental investment \((B = -0.12, SE = 0.05, p = .07)\) and sex and propensity towards taking reproductive risks \((B = -0.15, SE = 0.06, p = .01)\) (see Figure 3.2) were significant or approaching significance with the association between the predictor and desired number of offspring stronger for female participants.
3.5 Discussion

Our results showed that, amongst my sample, perceptions of environmental risk were significant predictors of adolescents' ideal AFB. I found that the adolescents in my study who have shorter perceived life expectancies favour earlier reproduction. To my knowledge this is the first study to
show an association between an individual’s SLE and their ideal AFB. This finding suggests that
that an individual’s perception of mortality is as salient as their perception of more general
environmental risk. My interpretation of this finding is that individuals are potentially able to
monitor the mortality risk of their environment by means of their SLEs, and are adjusting their
ideal AFB accordingly. However, my research is only suggestive of a causal pathway and more
research should be conducted.

I also showed that the safer adolescents judge their neighbourhood environment to be, the later
their reported ideal AFB. This result is supported by previous research (Johns, 2011), which
found that a woman’s subjective perception of risk in her environment is a more discriminating
predictor of her chance of becoming a teenage mother than neighbourhood economic
indicators. Interestingly, school risk was also significantly associated with ideal AFB in the
opposite direction as predicted, with an increase in perceived school risk predicting later
reproduction. This may be because, unlike an individual’s home environment, schools are
largely a chosen environment after age 16 in the UK. Perceived school risk might be a more
salient predictor of ideal AFB at younger ages, as individuals who view their school environment
negatively might be more likely to drop out and pursue childbearing as an alternative to
educational attainment (Fergusson & Woodward, 2000). Furthermore, the attitudes taught
directly or indirectly (from peers) in schools, might be a better indicator of subsequent
developing ideas on reproductive behaviour and attitudes. Previous research has shown that
school level characteristics are associated with individual behaviours, such as age of first
intercourse (Besarman & Brucker, 2001).

In my model the IMD for the local area of the school, a structural component of environmental
quality, which has previously been shown to be a strong predictor of AFB both between and
within populations, (Chipman & Morrison, 2013) did not significantly predict AFB nor did
individuals’ SES. While it is unexpected that SES did not predict ideal AFB it is possible that IMD as a school level variable was not sensitive to the variations in deprivation between immediate neighborhoods. The local rate of teenage pregnancy, however, did predict AFB, with higher rates associated with earlier reproduction. There was also a significant interaction with the association between the teenage pregnancy rate and AFB stronger for male adolescents. Furthermore, there was a significant sex by SES interaction, with the association between SES and ideal AFB being stronger for females with lower SES and predicting early reproduction.

The results of my model show the importance of accounting for individuals’ perceptions of their environment, in addition to objective measures of deprivation, when examining early childbearing and differences in AFB. This concurs with Johns (2011) and Upchurch, Aneshensal, Sucoff, & Levy-Storms (1999) who demonstrated that experiential neighbourhood perceptions were as important in predicting adolescent sexual activity as structural neighbourhood components. While I have called these measures of environmental risk, it may be possible that the measures of school and environment risk used partially tap into participants’ perceptions of social cohesion and collective efficacy (see Sampson, 2003). Therefore, it is possible I was showing an association between limited positive neighbourhood characteristics (such as supportive, trustworthy neighbours) rather than negative neighbourhood characteristics (such as fear of personal safety). An area for further research is whether social support or measures of perceived disorder are more salient in predicting individuals’ fertility intentions.

Less perceived environmental and school risk also predict a greater number of desired offspring in my study. This suggests that the participants want fewer offspring when they perceive their environment to be uncertain and unsafe. This association was stronger for female adolescents. On the other hand, previous research has been conducted on mortality salience and the desire for offspring which found that individuals primed to think about their own mortality reported
wanting more children. While an individual’s perception of their own mortality, as measured by the SLE, was not a significant predictor of wanting more offspring there was a significant sex by SLE interaction with the association stronger for male adolescents. Other studies examining mortality salience and desired offspring in particular, have found the association strong for males not females (Mathews & Sear, 2008). My findings, along with previous research, potentially point to different associations between a desire for offspring and perceptions of general environmental quality and perceptions of mortality. My findings also potentially suggest an important difference between the sexes in light of these perceptions, in terms of increasing individuals’ desires to procreate. This is another area where further research is needed.

The finding that SES was approaching significance as a predictor of ideal number of children is potentially controversial as politicians and the media in the United Kingdom claim that women from economically deprived areas conceive a greater number of children from early ages in order to increase their opportunities for child and housing benefits (see Dickins et al., 2012 for a discussion). However, more research needs to be conducted, with more representative samples, before these claims can be definitively supported or rejected, particularly as the structural components of environmental quality (IMD and teenage pregnancy rate) were not significantly associated with desired number or offspring.

Turning to the domain of kin networks, grandparental investment was marginally associated with adolescents’ future reproductive intentions, with closer relationships with grandparents predicting later ideal AFB. In addition, there was a significant sex by grandparental investment interaction, with the level of grandparental investment a stronger predictor of the ideal AFB of female adolescents in my sample. This goes against the prediction that those distant from grandparental and kin networks may perceive the cost of childrearing to be much greater, and therefore choose to delay reproduction until they are in a secure financial position and able to
afford child caring assistance from non-kin (Sear & Dickins, 2010). However, as has been
discussed (see Taylor, 1993), there is also the possibility that the close kin networks that may
promote cooperative breeding efforts may instead lead to resource competition between kin that
undermines any cooperative benefits. Close kin ties that span multiple generations may also
signal a low mortality environment consistent with later AFB (Low, Hazel, Parker & Welch,
2008). On the other hand, adolescents in my sample who reported more grandparental and
parental investment want more children. There was also a significant sex by parental investment
interaction, with a stronger effect of parental investment on increasing the desired number of
offspring for male adolescents. This suggests that grandparents may potentially offer individuals
assistance in terms of childrearing support and expertise, which does lend support to the idea
that close kin ties can embed adolescents in a cooperative breeding network. Whether or not
close kin networks promote or hinder cooperative breeding is an area that needs more research
to further my understanding of this complicated and multifaceted association. There are two
directions of study I propose to shed more light on these issues of kin support and reproductive
intentions. The first is what role physical proximity plays in understanding the impact of
grandparental investment. Research on a Dutch cohort found that maternal grandparents were
more likely to maintain frequent contact with their grandchild as the geographical distance
between them increased (Pollet, Nettle, & Nelissen, 2006). Further research should look into
what effect physical proximity has on levels of parental investment to further understand the
opposing theories regarding associations between competition, kin investment and any direct
reproductive benefits. Not living in close proximity with kin would perhaps remove direct
resource competition which would potentially increase the kin directed benefits from being
embedded in a cooperative breeding network. Secondly, examining different categories of
grandparents together (maternal and paternal) may be masking the different influences each
can have on grand-childbearing and fitness. In general, evolutionary studies have documented
differential levels of investment in grandchildren based on genetic relatedness and the sex of the grandchild (Fox et al. 2011).

Adolescents who favoured future rewards over immediate rewards reported wanting fewer offspring. The association with discount preference was also approaching significance for the adolescents’ ideal AFB. The link between fertility scheduling and future discounting is already well established (Daly & Wilson, 2005) and my findings offer additional support for the concept that there is a trade-off between reproductive effort now and parenting effort in the future (Gangestad & Simpson, 2000). Individuals who perceive the future as dangerous may take the immediate reward rather than wait for an uncertain return. In the same way they may desire more children because not all may survive, or intend to reproduce now rather than later. Those for whom the future holds more perceived opportunity can afford to wait for a bigger monetary payoff and to invest more in fewer offspring whom they are confident will survive and reproduce.

There was a significant interaction between sex and discount preference with the association stronger for males in my sample. This might represent different levels of investment in future offspring between males and females, due to sex differences in potential reproductive rates (Clutton-Brock & Parker, 1992). Men have the potential to reproduce faster, and as a result may have to compete more for mating opportunities with energy spent providing parental care potentially limiting their mating opportunities and their potential reproductive rate. Women on the other hand, have lower potential reproductive rates as mating opportunities may result in a substantial investment of time, energy and resources if a child is conceived. Such patterns of risk taking, and strategic trade-offs, would fall in line with predictions put forward in the framework of life history theory.

Adolescents who wanted more offspring reported being less likely to take reproductive risks and also viewed such behaviours as more risky, suggesting that risk taking is a rational strategy to
maximize reproductive success. There also is a significant sex by perceived reproductive risk interaction, with the association stronger for female adolescents. Successful reproduction represents a substantial investment for women. Furthermore, women have a limited reproductive career in which to successfully bear offspring. Therefore, if a woman wants more children it would be rational for her to limit the reproductive risks she exposes herself to so that she has an opportunity to have the number of offspring she desires within a relatively limited time frame compared to the opposite sex. Adolescents who want a greater number of children also view items on the mating risk taking scale as less risky. This could indicate more willingness to engage in sexual activity, or stronger pro-natal norms associated with their desire for offspring. Adolescents with a later ideal AFB report a greater likelihood of taking reproductive risks than their peers in my study. However, there was no difference in perceived riskiness, suggesting that these individuals recognize the risk inherent in their behaviour. These results suggest that adolescents in my sample who were less interested in reproducing were more likely to take reproductive risks. Perhaps they were less concerned with the potential impact such risks would have on their reproductive potential.

It would be useful here to reiterate that while it is best to think of individuals as placed on a fast to slow life history continuum, this framework, relates to the timing of reproductive decisions and it is more problematic to put mating or parenting strategies on a fast to slow continuum. This may in part explain why the results differ for AFB and desired number of potential offspring in my models. Mating and parenting strategies might be more gender specific as discussed here as trade-offs and payoffs are different for males and females.

Subjective KSSP (indicating stronger pro-natal and anti-contraception use norms) as opposed to objective KSSP (indicating factual knowledge of safe sexual practice), predict adolescents in my sample reporting a desire to have more offspring. There was also a significant sex by
subjective KSSP interaction associated with ideal AFB. Male adolescents with higher scores of subjective KSSP have an earlier ideal AFB. These findings potentially support the notion that adopting early reproduction and fast life history norms may not be due to gaps in adolescents’ knowledge or understanding of sexual risks, but rather that pro-natal norms develop in line with the type of behavior that will most assist in their reproductive success. My model also indicates that adolescents’ scores on the objective KSSP scale trend towards significance with more factual knowledge of safe sexual practice predicting ideal AFB. More research should be conducted to determine if adolescents with fast life history strategies have not only developed stronger pro-natal norms, but also have gaps in understanding of sexual risks, as this would have considerable policy implications. It is possible that my measure of subjective KSSP does not actually index subjective attitudes, potentially measuring nuanced facts not captured by the objective KSSP measure. However, there was no significant correlation between the objective and subjective KSSP measures. In addition, objective measures were chosen only if they had a correct or incorrect response while I would expect adolescents to have differing attitudes towards the questions on the subjective KSSP measure. There is potential to develop a better model of individuals’ subjective attitudes of safe sexual practice.

The data collected had a number of limitations thereby making my conclusions tentative about the proximate mechanisms influencing early childbearing and any causal pathways. Firstly, my outcome measures only reported desired age of first birth and marriage and desired number of children. Stated ideals may be different from actual future behaviour. However, as described in the Method section 3.3, previous research indicates that ideal age of parenthood is established by age 16 and does go on to predict subsequent behavior (Nettle et al., 2011). This suggests that examining adolescents’ reported ideals is a useful way to gauge future fertility intentions and that it does have implications for real-world decisions. Furthermore, it is of interest not only to look at actual behavioural outcomes, but also to examine the psychology of intentions.
Secondly, there may be some debate over my differentiation between subjective and objective measures of environmental risk and knowledge of safe sexual practice. However, as the scope of my study was to examine the social-psychological associates of early fertility intentions, I would argue that adolescents’ views are an important consideration. As I show with my model, adolescents’ perceptions of the quality of their environment and their own mortality were often better predictors of their fertility intentions than structural components of environmental quality.

Thirdly, even when all variables were entered into the model, they only account for a minority of the variance. Finally, and more generally, my study is cross-sectional, rather than longitudinal, so that associations between ideal fertility intentions and the factors detailed here may be the result of unmeasured variables rather than a direct causal relationship. In addition, I have a convenience sample that is relatively small compared with many demographic studies. Therefore, a number of non-significant correlations may simply be due to low power.

Furthermore, as the sample is not random nor probability sampled from Hampshire or the United Kingdom, the capacity for generalization is low. However, while I would not be justified in making generalized statements my aim is primarily to explore the psychology of intentions, exploring the relationships between individuals’ social-psychological attitudes and their ideal reproductive outcomes.

Despite these limitations, my findings are at least suggestive in helping understand early childbearing and the increased risk of teenage pregnancy in the United Kingdom. My study is relatively unusual in that it also studies the fertility intentions of male adolescents. In addition, this study confirms the findings of Nettle & Cockerill (2010) that showed few differences between the sexes in terms of ideal fertility intentions or the effects of predictors on those intentions. My findings supported an evolutionary perspective which suggests that the local environment is driving early fertility through calibrated reproductive intentions based on perceived environmental risk. The findings on whether young people are embedded in
cooperative kin networks that support fast life history norms, or whether these close networks actually support slower life histories, cannot be fully determined here. It would be of interest to investigate such alternatives further. Furthermore, most risk taking behaviour can be viewed as a rational response to individual intentions and potentially to environmental uncertainty. To effectively target early childbearing, attempts should be made to reduce perceptions of relative poverty and extrinsic mortality risks. Most policies currently employed to prevent teenage pregnancy often ignore the fact that many young women may be choosing to have children while they are in good health and can rely on available kin support (Geronimus, 1996). Policies on early reproduction must recognize the importance of life history trade-offs as core to reproductive scheduling. Such methods are not only more likely to succeed but also more likely to have a lasting effect on reversing the rate of teenage pregnancy in areas that are persistently at risk and, importantly, on improving the life situations of adolescents and adolescent parents.
Chapter 4

Experimentally induced stress influences ideal female reproductive timing

4.1 Overview

Accumulated evidence suggests that a chronic exposure to stress is associated with an earlier age of reproduction in humans. The majority of this research, however, is correlational and does not prove that high stress causes an accelerated onset of female reproductive ideals. I propose that acute stress has the potential to influence an individual’s reproductive ideals and that the way an individual responds to stress depends on their adaptive life history strategies shaped by their exposure to chronic stressors. In order to directly test this I ran cold-pressor tasks (a laboratory paradigm that induces acute stress) designed to activate both the autonomic nervous system and the hypothalamic-pituitary-adrenal axis and examined the effect of acute stress on females’ reported reproductive ideals. My results show that acute stress caused the participants in my study to shift their ideal age of first birth and marriage to earlier ages. I also explored competing hypotheses, testing whether acute stress had a more general impact on females’ time preference, prosocial tendencies, parental investment strategies, risk taking propensity and
sociosexual desire. Furthermore, I show there is an interaction between an individual’s exposure to chronic stress during childhood and exposure to the cold-pressor task in terms of their reproductive ideals. Individuals who reported more exposure to early childhood stress responded to the acute stress condition by reporting earlier ideals. These findings offer the first experimental evidence that stress can alter female’s reproductive decision making.

4.2 Introduction

Natural selection favours a point where the costs and benefits of reproductive trade-offs are optimized, however, focusing solely on this ultimate approach to human behaviour ignores the links between particular ecologies and behavioural responses. An equally important approach to human behavioural variation is the study of the proximate mechanisms that connect specific ecologies with behavioural responses. There seem to be various triggers for the onset of early reproduction (Coall & Chisholm, 2003; Ellis, Essex, & Boyce, 2005) in humans. One particular area of interest is the relationship between the onset of reproduction and individual stress responsivity which includes both the working parameters of the stress responsivity system (baseline activation of hormone levels) and in its responsivity to external events (the magnitude of cortisol response or the balance between sympathetic and parasympathetic activation).

In an attempt to unify the theoretical framework for the study of individual differences in stress responsivity and how such differences are conditionally adaptive, Del Giudice, Ellis and Shirtcliff (2011) proposed the Adaptive Calibration Model. This model explores how one of the main biological functions of the stress response system is to regulate an individual’s physiology and behaviour in a number of fitness related areas including reproduction. The main premise of the Adaptive Calibration Model is that individual differences in stress responsivity are the result of
the evolved ability of an individual to modify their developmental trajectory and as a consequence their resulting phenotype to match local social and environmental conditions.

There are four main stress response profiles that the authors of the Adaptive Calibration Model propose. Of most interest to the current study are the predicted profiles of individuals exposed to low stress and safe environments who exhibit high stress responsivity and have a Sensitive stress profile, and individuals who are exposed to high stress and unsafe environments who also have high stress responsivity in response to these challenges and have a Vigilant stress response profile (see figure 4.1). Individuals exposed to moderate levels of developmental stress are proposed to have a Buffered stress response profile and demonstrate lower stress responsivity relative to the Sensitive and Vigilant stress response profiles while individuals exposed to severe and traumatic stress might have an Unemotional stress response profile with limited physiological responses to stress cues.
Because the stress response system is highly plastic, particularly during early development (Boyce & Ellis, 2005; Levine, 2005), stress is a likely candidate for a proximate mechanism that adjusts individuals’ life history strategies. The main body of research examining this association in humans, however, is correlational and focused on chronic, historical stress as opposed to acute, short-term stress (Belsky, Steinberg, & Draper, 1991; Bogaert, 2008; Nettle, Coall, & Dickins, 2011; Quinlan, 2003). Here, I go further and look at how acute stress may have the
potential to cause similar behavioural shifts and how this may cause differences in behavioural variation for individuals with different stress response systems.

Thus, in the work described in this chapter, I examine evidence suggesting that exposure to chronic stress has an influence on reproductive timing and individuals’ ideal age of first birth. Furthermore, I consider the possibility that acute stress may also have the potential to calibrate potential reproductive timing. I also investigate the interaction between exposure to chronic and acute physiological stress; specifically whether women exposed to different levels of stress during childhood development may react differently to acute stress in terms of adjusting their fertility intentions. If so, this would suggest that exposure to both repeated stressors and high stress events can alter women’s reproductive timing. Using an experimental approach, I investigate the impact of acute stress and its reaction of self-reported chronic stress on women’s reported fertility intentions.

### 4.2.1 Chronic stress and reproductive timing

One of the fundamental factors affecting the development of an individual’s life history is resource availability. Different levels of energetic stress such as, malnutrition, low energy intake, negative energy balance, and associated internal stressors such as disease all affect developmental processes, including the development of behavioural strategies such as the timing of reproduction (MacDonald, 1999; Ellison, 2001). Resource availability can also alter the development of individual stress response systems. For example, maternal calorific restriction in rats has been shown to result in epigenetic changes in their offspring’s hypothalamic-pituitary-adrenal axis which controls secretion of the stress hormones such as cortisol (Meaney, 2010).
Once an individual has adequate energetic resources to support somatic growth and development, other extrinsic environmental conditions such as harshness (high morbidity-mortality regimes) and unpredictability affect their life history strategy (Ellis Figueredo, Brumbach, & Schlomer, 2009). Environmental cues of high morbidity and mortality adjust behavioural strategies towards early reproduction, conveyed by frequent sympathetic nervous system activation as the stress response system signals the potential dangers of the surrounding environment (Del Giudice, et al., 2010).

Therefore, encountering stressful environments and dealing with chronic stressors in childhood direct an individual towards strategies that are adaptive under ecological conditions (Ellis, Shirtcliff, Boyce, Deardorff, & Essex, 2011). The sensitivity of the stress response system to the chronic ecological stress suggests that cortisol plays a central role in the regulation of these strategies. In the case of the onset of reproductive timing and early age of first birth, females must begin a suite of hormonal and growth changes by middle childhood to successfully reach menarche in preparation for childbearing at younger ages. Since cortisol is a major regulator of sexual development and fertility, experiences of environmental stress may influence the reproductive axis at key switch points during development and puberty (see Ellis, 2004 for a review).

Moreover, exposure to chronic stressors caused by low early life investment has a profound effect in the development of individual stress responsivity. In non-human species, experimental work has firmly established the causal link between low early-life investment and altered stress physiology through manipulation of levels of rats’ maternal grooming and licking of their pups (Bagot et al., 2009). In humans, exposure to maternal stress is associated with the developing stress physiology and temperamental reactivity of the foetus (Gutteling, Weerth, & Buitelaar, 2005; O’Connor et al., 2005). During childhood, familial stress predicts adrenarche or early
pubertal development (Ellis & Essex, 2007), and the extent of conflict, instability and rejection experienced in a familial environment is strongly linked with a child’s hypothalamic-pituitary-adrenal response (Flinn, 2006). Furthermore, experiences of agonistic stress in adolescence predicted subsequent early fertility and having a child outside of marriage (Davis & Werre, 2007).

The obvious limitation of the majority of these findings is that they are correlational in nature. However, there is some evidence from natural experiments, including one study of the reproductive behaviour of women in Helsinki after large scale evacuations due to the Second World War. As evacuations were for the most part decided randomly with respect to family characteristics, this is a quasi-experimental design between those individuals who were evacuated away from their birth families and those individuals who remained (Pesonen et al., 2008b). Women who had arguably experienced greater chronic stress due to being evacuees had earlier ages of menarche and more children in total that the non-evacuated controls, although, interestingly, age of first birth was not significantly earlier. These findings suggest that early familial stress is particularly salient to the development of an individual’s life history strategies and may well have an impact on the onset of reproduction.

4.2.2 Acute stress and reproductive timing

While the causal relationship between chronic stress and age of first reproduction is still relatively unexplored, the effects of acute stress on life history strategies are even less well known. Furthermore, definitions of what is meant by the term stress often differs from one study to the next which may have implications for the interpreting results. For example, there are a limited number of experimental studies that have begun to examine causal links between
psychological stress as induced through mortality priming and life history strategies. One key paper recently published demonstrated that across a series of experiments exposure to stress altered people’s preferences for both ideal age of first birth and ideal age of marriage. Furthermore, the effects of stress exposure depended on the extent to which people had a stressful childhood (Griskevicius, Delton, Robertson, & Tybur, 2011). There are, however, two potential limitations of this work. Firstly, the authors manipulated individual’s perceptions of danger, having people read a news article about increasing mortality rates and were thus potentially measuring individual’s exposure to psychological stress instead of a purely acute physiological stress response as such the researchers cannot be sure they measured a stress response removed from any other psychological or social mechanisms. The only measures of stress obtained were participants’ subjective ratings of their own stress with no evidence of the participants having experienced physiological arousal. Secondly, this research measured childhood stress using childhood socioeconomic status. While childhood socioeconomic status is likely indication of exposure to exposure to chronic stressor during development, research suggests that individual’s subjective perceptions of the environmental quality are stronger predictors of fertility intentions (Chipman & Morrison, In Press) and reproductive timing (Johns, 2011).

In addition, experimental manipulations in psychological studies have found that priming mortality influences reproductive goals in terms of increasing the desired number of offspring for males (Mathews & Sear, 2008) and for females, when controlling for career ambitions (Wisman & Goldenberg, 2005). The underlying proximate mechanisms at work in such human studies are not known, but a plausible suggestion is activation of stress response systems, as the hypothalamic-pituitary-adrenal axis responds strongly to challenging and uncontrollable threats (Dickerson & Kemeny, 2004). These findings are corroborated by demographic studies which
have shown that real life high stress events, such as acts of terrorism or natural disasters, are followed by local fertility spikes (Cohan & Cole, 2002; Rodgers, John, & Coleman, 2005).

Acute stress has also been shown to impact an individual’s propensity towards risk taking behaviour (Lighthall, Mather, & Gorlick, 2009; van den Bos, Harteveld, & Stoop, 2009). This is consistent with predictions made by life history theory: increased cues of environmental risk should promote high-risk taking and a preference for immediate over delayed rewards (Chisholm, 1999a; Wilson & Daly, 2006). Thus an individual exposed to acute stress may be more likely to have present, rather than future, orientated preferences.

Furthermore, experimental studies have demonstrated that elevated cortisol levels and activating the hypothalamic-pituitary-adrenal axis influences male mate preference (Lass-Hennemann et al., 2010). In females, exposure to a social stressor demonstrated a relationship between cortisol reactivity and age of first intercourse (Brody, 2002). Women with an earlier age of first intercourse (a potential hallmark of a fast life history strategy) had increased cortisol levels in response to the stress task compared with women with older ages of first intercourse (possibly on a slower life history trajectory). Thus it is reasonable to predict that firstly, acute stress has the potential to influence an individual’s life history strategy and secondly, the way an individual responds to stress depends on their life history trajectory.

This prediction is in line with previous studies of animal behaviour. Lancaster, Hazard, Clobert, & Sinervo (2008) looked at reproductive behaviour in female side-blotched lizards Uta stansburiana who have evolved both slow and fast life history strategies. By administering corticosterone treatment to the female lizards, they discovered that the slow strategists delayed reproduction, while for the fast strategists reproduction was enhanced. Likewise in humans, individuals on different life history trajectories might respond in similar ways to the presence of
acute stress. That is to say, there might be an interaction between how individuals respond to acute stress based on their previous exposure to chronic stress. Although, to my knowledge, the interaction between acute stress and chronic stress has not been directly tested in humans in terms of hypothalamic-pituitary-adrenal and cortisol responsivity, research has found that social stressors, such as a female-biased sex ratio, is associated with differential life history strategies in terms of fertility scheduling in females (Chipman & Morrison, 2013).

### 4.2.3 Research overview

I conducted two studies to experimentally examine the effect of acute stress on females’ life history preferences. As it is uncertain whether or not psychological priming studies activate a physiological response my measure of acute stress would involve focusing on individual’s response to a pure physiological stressor. On the basis of previous experimental research (Griskevicius, Delton, Robertson, & Tybur, 2011; Mathews & Sear, 2008; Brody, 2002; Lancaster et al., 2008), as well as observation of real world responses to both high stress events (Cohan & Cole, 2002; Rodgers et al., 2005), and prolonged environmental stressors (Davis & Werre, 2007; Ellison, 2001) my core prediction is that acute stress will accelerate female life history preferences, and that there will be an interaction between that effect and the individual’s previous exposure to chronic stressors during childhood development such that individuals with higher reported levels of exposure to early childhood stress might have strong stress response patterns to acute stress causing them to report different ideals than individuals with lower levels of reported early childhood stress.

In Study One, I manipulated women’s exposure to an acute stressor and looked at individual responses to acute stress and reported ideal age of first birth, ideal age of marriage and desired
number of children. In addition, I looked at the impact of acute stress on other life history preferences such as parental investment strategies, propensity towards risk taking behaviour and attitudes to uncommitted sex and sociosexual desire. In Study Two, I looked at whether or not an individual’s psychological responses to acute stress were specific to reproductive time preferences or part of a more general shift in an individual’s time horizon towards immediate gains and discounting of the future. I also looked to establish whether an individual mislabels their physiological arousal as desire for social comfort, which may increase their desire to have a husband and/or a child more immediately. Finally, in a follow up study I looked at whether there is an interaction effect between chronic and acute stress and what impact this might have on an individual’s life history strategies. By using experimental techniques I hope to look causally at the impact that stress has on potentially adjusting female life history preferences.

4.3 Study One: Acute stress and life history preferences

The first step in examining the link between acute stress and life history preferences was to run a cold-pressor stress paradigm to assess the effect of acute physiological stress on female reproductive timing ideals, parental investment strategies, propensity to risk taking behaviour and more generally their attitudes toward uncommitted sex. I predicted that there was unlikely to be any shift in females’ risk taking behaviour or attitudes towards uncommitted sex as less risk taking in women than men has been observed across a wide range of behaviours (d’Acremont & Van der Linden, 2006). I also predicted that I may not find any difference in parental investment strategies or participants’ desired number of children, as previous studies have found little change in female participants due to experimental manipulation (Mathews & Sear, 2008). However, I did predict a shift in ideal reproductive timing due to the stress manipulation.
4.3.1 Methods

4.3.1.1 Participants

70 non-smoking female undergraduates (mean age 18.93 years ±2.10) were recruited. Participants were required to refrain from consuming alcohol, caffeine drinks or food for one hour before beginning the experimental session.

4.3.1.2 Design and procedure

The socially evaluated cold-pressor or ice-water test is a commonly used and well validated laboratory pain stressor which has been shown to activate both the autonomic nervous system and the hypothalamic-pituitary-adrenal axis (Schwabe, Haddad, & Schachinger 2008). The cold condition increases cortisol responses significantly more than the warm condition. This rise in cortisol starts about 5 minutes after the triggering event with a peak between 10 and 30 minutes.

Experimental sessions were run between 14.00 and 17.00 to control for diurnal cycle of cortisol. Each session lasted approximately 30 minutes. When each participant arrived for the experiment, they were asked to be seated at a table and chair with their non-dominant hand adjacent to the basin used for the test. After each participant signed the consent form and completed the pre-measure and demographic questions, I attached heart rate monitors and a sphygmomanometer was attached to their dominant arm. Participants’ heart rates were recorded for 90 seconds and two baseline blood pressure readings were taken. Next, I randomly assigned participants to the cold water stress condition or a warm water non-stress
condition. Due to technical problems during data acquisition, heart rate data for two participants in the ice water condition and five participants in the warm water condition were missing.

(i) Stress-condition: cold-pressor test

The experimenter informed the participants assigned to the stress condition that they would be immersing their hands in ice water for up to 3 minutes, or for as long as they could tolerate. They were informed that the procedure would potentially be unpleasant and cause discomfort. The experimenter asked the participant to insert their non-dominant hand into the basin of ice water (maintained at 0–4 °C), up to their wrist, with their palm facing the ceiling. The participants were informed not to make a fist with their hand. Three participants withdrew their hand from the ice water before the 3 minute limit. The experimenter measured the participants’ blood pressure immediately after they immersed their hand in the ice water, and then at 1 minute intervals until the participant removed their hand from the water. All participants had three blood pressure readings taken at 1 min intervals during the ice water hand immersion except for the three participants who removed their hands from the ice water before the 3 minutes, who had one blood pressure reading taken. Continuous heart rate readings were recorded electronically for each participant at 15 second intervals.

(ii) Non-stress condition: warm water test

I informed the participants they would be immersing their hand in water maintained at normal body temperature (35–37 °C) for 3 minutes. Participants placed their non-dominant hand into the basin of warm water up to their wrist with their palm facing the ceiling. The participants were informed not to make a fist with their hand. All participants kept their hand in the warm water for the full 3 minutes. Cardiovascular data were recorded as with the cold condition.
Immediately after the participants withdrew their hands from either condition, the experimenter prompted them to rate separately how stressful, unpleasant and painful the previous hand immersion had been on scales ranging from 0 (not at all) to 100 (very) in 10-point increments. After the subjective ratings were complete, participants’ heart rates were measured for 90 seconds and a post-measurement blood pressure reading was taken. Once this was done, the participants completed the experimental measures.

### 4.3.1.3 Manipulation checks

Physiological and subjective measures indicated that the cold-pressor condition did in fact cause the participants physiological stress in contrast to the control condition. Cardiovascular data showed that participants’ heart rates \( t(59) = 2.90 \ p = .005, \eta^2 = 0.12 \), systolic \( t(64) = 6.20 \ p < .001, \eta^2 = 0.33 \) and diastolic \( t(64) = 7.44 \ p < .001, \eta^2 = 0.45 \) blood pressure readings were significantly elevated in the cold condition only during the hand immersion. Participants in the cold-pressor condition rated the procedure as significantly more stressful \( t(68) = 8.60 \ p < .001, \eta^2 = 0.52 \), unpleasant \( t(68) = 15.75 \ p < .001, \eta^2 = 0.78 \) and painful \( t(68) = 15.03 \ p < .001, \eta^2 = 0.77 \) than participants in the warm water condition (see Table 4.1).
**Table 4.1** Mean (SD) subjective stress ratings and cardiovascular measures before (pre), during and after (post) hand immersion in the warm water or cold water conditions

<table>
<thead>
<tr>
<th></th>
<th>warm water condition</th>
<th>cold-pressor condition</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Subjective stress ratings (0-100)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>stressful</td>
<td>7.94 (13.88)</td>
<td>51.94 (26.60)**</td>
</tr>
<tr>
<td>unpleasant</td>
<td>10.00 (17.06)</td>
<td>79.72 (19.78)**</td>
</tr>
<tr>
<td>painful</td>
<td>4.41 (12.36)</td>
<td>70.56 (22.67)**</td>
</tr>
<tr>
<td><strong>Heart rate (beats per minute)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pre</td>
<td>77.82 (11.74)</td>
<td>83.03 (9.86)</td>
</tr>
<tr>
<td>during</td>
<td>78.32 (11.51)</td>
<td>87.06 (11.95)*</td>
</tr>
<tr>
<td>post</td>
<td>80.14 (10.61)</td>
<td>80.34 (9.36)</td>
</tr>
<tr>
<td><strong>Systolic blood pressure (mm Hg)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pre</td>
<td>107.01 (11.50)</td>
<td>110.21 (10.37)</td>
</tr>
<tr>
<td>during</td>
<td>105.18 (12.18)</td>
<td>122.11 (9.88)**</td>
</tr>
<tr>
<td>post</td>
<td>104.62 (11.31)</td>
<td>107.47 (9.68)</td>
</tr>
<tr>
<td><strong>Diastolic blood pressure (mm Hg)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pre</td>
<td>65.13 (7.96)</td>
<td>67.76 (8.64)</td>
</tr>
<tr>
<td>during</td>
<td>64.93 (7.42)</td>
<td>80.41 (9.45)**</td>
</tr>
<tr>
<td>post</td>
<td>64.32 (7.96)</td>
<td>65.67 (9.75)</td>
</tr>
</tbody>
</table>

*<p<.05 compared with the warm water condition

**<p<.001 compared with the warm water condition
4.3.1.4 Dependent measures

Parental investment strategies were determined using a measure of the costs and benefits of children developed as part of a mortality priming psychological study (Mathews and Sear, 2010). There were 15 items coded on a 9-point scale where 1 equalled Strongly Disagreed and 9 equalled Strongly Agreed. Higher scores indicate that children were perceived to be more beneficial than costly.

Aspects of risk taking were measured using the evolutionarily valid domains of risk scale developed by Kruger, Wang, & Wilke (2007). I used the mating domain which measured interpersonal behaviour and resource allocation for mate attraction. I also used the reproductive domain which looked at trade-offs between resources and fertility. For each domain, three items were used and participants were asked how risky they perceived each item presented to be and how likely they would be to engage in that behaviour on a five point bipolar scale. Higher scores indicate higher likelihood of engaging in the risky activity and lower perceived riskiness.

Attitudes toward uncommitted sex and sociosexual desire were measured using the nine item revised Sociosexual Orientation Inventory (SOI-R) (Penke & Asendorpf, 2008). Answers to each statement were given using a nine point scale, which were coded and aggregated to form a behaviour facet (Cronbach’s alpha = 0.85), an attitude facet (Cronbach’s alpha = 0.87) and a desire facet (Cronbach’s alpha = 0.86). All nine items were then aggregated to a total score of global sociosexual orientation (Cronbach’s alpha = 0.83). Cronbach’s alpha is a coefficient of internal consistency for psychometric tests with higher scores indicating greater reliability.

Finally, participants completed a free text response to the questions; ‘At what age do you want to have your first baby?’, ‘What would be the ideal number of children you want to have?’, and ‘At what age do you want to get married?’ Individuals’ stated fertility intentions were used as a
proxy measure of actual reproductive scheduling based on Nettle, Coall and Dickins’ (2011) investigation of data from the National Childhood Development Study. This investigation showed that at the onset of adulthood (age 16), individuals have formed conscious intentions regarding their ideal timing of parenthood. Furthermore, the responses women gave were strong predictors of their actual ages of conception and childbearing even when the event occurred years later.

All dependent variables as well as age, contraceptive use and stage of the menstrual cycle were entered as between subject factors into independent t-tests.

4.3.2 Results & discussion

There was a significant main effect of stress condition on ideal age of first birth and marriage. In the cold-pressor stress condition ideal age of first birth was 26.9 years, compared with 28.6 in the warm condition \( t(64) = 3.19, p<.001, \eta^2 = 0.14 \) and ideal age of marriage from was 25.3 and 26 years, respectively (unequal variances assumed \( t(64) = 53.4, p<.001, \eta^2 = 0.15 \)). Ideal age of marriage and ideal age of first birth were strongly correlated \( r = 0.714, p<.005 \). There was no significant difference in ideal age of first birth \( t(60) = 1.93, \text{ns} \) or marriage \( t(61) = 0.49, \text{ns} \), regardless of whether the individual was on the follicular or luteal stage of their cycle or whether they were using contraceptives or not \( t(58) = 1.37, \text{ns}; t(60) = 0.27, \text{ns} \), respectively. These findings indicate that the cold-pressor task caused women to want to get married and have children sooner. Given that the average age was 18.93, the difference of 1.7 years equals an 18% reduction, and the difference of 1.5 years equals a 19% reduction (see Figure 4.2).
There was no significant main effect of condition on parental investment strategies \( t(68) = 1.19, \) ns), desired number of children \( t(68) = 0.14, \) ns), global SOI \( t(68) = 0.14, \) ns) or on the likelihood of taking mating risk \( t(68) = 0.60, \) ns) or reproductive risks \( t(68) = 1.69, \) ns).

Descriptive statistics for the dependent measures are reported in Table 4.2.

**Figure 4.2** Mean (95% confidence Intervals) ideal age of first birth and ideal age of marriage.

Dark bars designate warm water condition; light bars designate cold pressor condition.
Table 4.2 Descriptive statistics for variables not significantly different between the warm water and cold pressor conditions. Data are means (SD) unless otherwise stated.

<table>
<thead>
<tr>
<th>Variable</th>
<th>warm water condition</th>
<th>cold-pressor condition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (18 to 31)</td>
<td>18.97 (2.24)</td>
<td>18.89 (1.99)</td>
</tr>
<tr>
<td>Contraceptive use (count of women using contraceptives)</td>
<td>17</td>
<td>24</td>
</tr>
<tr>
<td>Menstrual cycle stage (count of women on luteal stage)</td>
<td>15</td>
<td>20</td>
</tr>
<tr>
<td>Parental investment strategies* (-16 to 21)</td>
<td>1.21 (8.82)</td>
<td>0.56 (7.5)</td>
</tr>
<tr>
<td>Desired number of children (0 to 4)</td>
<td>2.47 (0.86)</td>
<td>2.44 (0.84)</td>
</tr>
<tr>
<td>Global SOI (10 to 69)</td>
<td>30.97 (14.20)</td>
<td>27.61 (8.89)</td>
</tr>
<tr>
<td>Likelihood of taking mating risks** (-6 to 6)</td>
<td>-2.85 (2.20)</td>
<td>-2.53 (3.31)</td>
</tr>
<tr>
<td>Likelihood of taking reproductive risks** (-6 to 6)</td>
<td>-4.71 (1.36)</td>
<td>-3.94 (2.28)</td>
</tr>
</tbody>
</table>

* higher scores indicate individuals view raising children as having more benefits than costs
** higher scores indicate greater likelihood of taking risks

Our findings suggest that physiological stress may be sufficient to shift women’s preferences towards early reproduction. I did not find any effect of physiological stress on the likelihood or propensity of females to undertake mating or reproductive risks, nor did the acute stress condition affect females’ attitudes towards uncommitted sex and sociosexual desire. This is in line with life history theory which suggests males are more likely to engage in risk taking behaviour as a life history strategy, whereas females are more likely to adjust their parental
investment strategies in response to stressors (del Giudice, Ellis, & Shirtcliff, 2011). However, as with previous research, I did not find any effect of the stress condition on the desired number of children nor on female parental investment strategies (Mathews & Sear, 2008). It would appear then, that acute stress has potential to adjust aspects of an individual's life history strategies, specifically the reported ideals in terms of reproductive timing and age of marriage.

### 4.4 Study Two: Acute stress, reproductive timing and more general effects

Study one revealed that acute stress has the potential to alter females’ stated intentions about their ideal reproductive timing. However, it is not obvious that physiological stress is regulating reproductive timing via the kind of behavioural response assessed here: a statement of the ideal time to reproduce. Rather, it may be that intentions about future reproductive timing are being calibrated through other routes, such as a more general shift in time preference. The effect observed in Study One could reflect, in a more general way, effects of stress on perceptions of time horizons, potentially leading individuals to focus more on present gains and losses, and discount the future. This would also make adaptive sense in a dangerous environment, where it is beneficial to obtain rewards now rather than wait for a better reward in the future which may be too late.

Additionally, perhaps following a physiological stress, some individuals seek social comfort, and my measures about whether one would want a husband or children may access that effect in an indirect way. Taylor et al., (2000) proposed that humans, specifically females, have a “tend and befriend” stress response designed to increase oxytocin levels and thereby reduce stress response. Arguably such a response may not be unique to humans. Animal studies have shown that treating wounded and socially isolated Syrian hamsters *Mesocricetus auratus* with
oxytocin eliminated the stress-induced increases in cortisol and facilitated wound healing. In addition, treating socially housed hamsters with an oxytocin antagonist delayed wound healing (Detillion, Craft, Glasper, Prendergast, & DeVries, 2004) Furthermore, recent research has found a similar effect amongst male participants, where acute social stress increased male prosocial behaviour participants (von Dawans, Fischbacher, Kirschbaum, Fehr, & Heinrichs, 2012).

In order to test these two alternative hypotheses against the prediction and findings of Study One, I ran a second cold-pressor paradigm to look at the effect of acute stress on a measure of general time preference, known as an individual's discount preference. I also examined their desire for social companionship following an acute stressor measuring the participant’s desire to go on a date with a number of potential male mates as well as their prosocial behaviour. In addition, I measured participants’ ideal age of first birth, ideal age of marriage, and desired number of children. I predict that if acute stress is calibrating female reported reproductive timing ideals, rather than a more general effect on time preference or prosocial behaviour, then I will only see a change in female’s reported ideal age of marriage and ideal age of first birth and not in the measure of prosocial behaviour or discount preference.

### 4.4.1 Methods

#### 4.4.1.1 Participants

63 non-smoking female undergraduates (mean age 20.82 years ±5.09) were recruited. Participants were required to refrain from consuming alcohol, caffeine drinks or food for 1 hour before beginning the experimental session.
4.4.1.2 Design and procedure

When each participant arrived, their heart rates were recorded for 90 seconds and two baseline blood pressure readings were taken. Next, I randomly assigned participants to the cold-pressor condition (n=29) or the control condition (n=34). They then immersed a hand into the basin of ice water (maintained at 0–4°C) for 3 minutes or for as long as they could tolerate. Three participants withdrew their hands from the ice water before three minutes. Excluding these participants from the analysis did not alter the results. In the warm condition, participants immersed their non-dominant hand into water (35–37 °C) for three minutes. Blood pressure was measured immediately after immersion, and then at 1 minute intervals until participants had removed their hands from the water. Heart rate readings were recorded electronically for each participant at 15 sec intervals.

Immediately after withdrawing their hands, participants rated how stressful, unpleasant and painful the immersion had been on scales ranging from 0 (not at all) to 100 (very) in 10-point increments. Their heart rates were then measured for 90 seconds and a post-measurement blood pressure reading was taken.

4.4.1.3 Manipulation checks

Cardiovascular data showed that participants’ heart rates (t(47) = 4.54 p<.001, η² = 0.31), systolic (t(63) = 7.65 p<.001, η² = 0.51) and diastolic (t(63) = 6.24 p<.001, η² = 0.42) blood pressure readings were significantly elevated in the cold condition only during the hand immersion. Participants in the cold-pressor condition rated the procedure as significantly more stressful (t(63) = 12.21 p<.001, η² = 0.70), unpleasant (t(63) = 29.77 p<.001, η² = 0.93) and
painful \( (t(63) = 28.85 \ p<.001, \ η^2 = 0.93) \) than participants in the warm water condition (see Table 4.3).

### Table 4.3

Mean (SD) subjective stress ratings and cardiovascular measures before (pre), during and after (post) hand immersion in the warm water or cold water conditions

<table>
<thead>
<tr>
<th></th>
<th>warm water condition</th>
<th>cold-pressor condition</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Subjective stress ratings (0-100)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>stressful</td>
<td>6.76 (13.19)</td>
<td>58.70 (26.61)*</td>
</tr>
<tr>
<td>unpleasant</td>
<td>5.29 (11.07)</td>
<td>85.48 (10.59)*</td>
</tr>
<tr>
<td>painful</td>
<td>1.76 (8.69)</td>
<td>77.74 (12.30)*</td>
</tr>
<tr>
<td><strong>Heart rate (beats per minute)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pre</td>
<td>79.20 (11.48)</td>
<td>85.12 (14.91)</td>
</tr>
<tr>
<td>during</td>
<td>77.75 (11.06)</td>
<td>91.91 (10.57)*</td>
</tr>
<tr>
<td>post</td>
<td>80.90 (10.84)</td>
<td>81.56 (10.99)</td>
</tr>
<tr>
<td><strong>Systolic blood pressure (mm Hg)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pre</td>
<td>108.82 (7.76)</td>
<td>109.64 (10.53)</td>
</tr>
<tr>
<td>during</td>
<td>108.41 (8.48)</td>
<td>126.50 (10.54)*</td>
</tr>
<tr>
<td>post</td>
<td>107.26 (8.42)</td>
<td>108.38 (11.94)</td>
</tr>
<tr>
<td><strong>Diastolic blood pressure (mm Hg)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pre</td>
<td>68.03 (7.77)</td>
<td>67.87 (10.31)</td>
</tr>
<tr>
<td>during</td>
<td>68.18 (13.27)</td>
<td>84.96 (13.27)*</td>
</tr>
<tr>
<td>post</td>
<td>68.18 (8.51)</td>
<td>68.19 (11.04)</td>
</tr>
</tbody>
</table>

*\( p<.001 \) compared with the warm water condition
4.4.1.4 Dependent Measures

Our measure of discount preference was based on a measure developed by Chesson, et al. (2006). Discount rates were calculated based on participants’ responses to three hypothetical questions about the possible payoff to a prize. In the first question, the participant was asked if they would prefer a prize of £400 today versus a prize of £1200 a year from today. In the second and third questions, the future prize was reduced to £800 and £500 respectively. From their responses, individuals were categorized from those who strongly favoured immediate gratification (1) to those who strongly favoured delayed gratification (6).

To measure self-reported prosocial behaviour, I used the 23-item Prosocial Tendencies Measure developed by Carlo and Randall (2002). This measure consists of 6 subscales: public (4 items, Cronbach’s α = 0.80), anonymous (5 items, Cronbach’s α = 0.88), dire (3 items, Cronbach’s α = 0.54), emotional (4 items, Cronbach’s α = 0.77), compliant (2 items, Cronbach’s α = 0.87), and altruistic (5 items, Cronbach’s α = 0.62). The scores from each sub-scale can also be combined to create a global measure of prosocial behaviour (Cronbach’s α = 0.83). Participants were asked to rate the extent to which statements described themselves on a 5-point scale ranging from 1 (does not describe me at all) to 5 (describes me greatly).

I also took a measure of each participant’s desire for companionship. To do this, each participant was shown 25 male faces and asked to respond yes/no as to whether they would like to date the individual shown. I recorded the number of yes responses each individual made as well as the response time, in milliseconds, that each participant took to make their decision. As a control, I showed participants images of 25 cars and asked them yes/no as to whether they would like to own the car shown. I recorded the number of yes responses each individual made,
as well as the response time each participant took to make their decision in milliseconds. I will not consider the results for the cars further as there was no difference between conditions.

In this second experiment, I again asked participants to complete free text responses to the following questions; ‘At what age do you want to have your first baby?’, 'What would be the ideal number of children you want to have?', and 'At what age do you want to get married?'

4.4.2 Results & discussion

There was no difference between conditions in terms of age, socioeconomic status, age of menarche, whether women were on their luteal or follicular stage of their cycle or contraceptive use. The cold-pressor stress condition reduced ideal age of first birth from 28.8 to 27.7 years (t(55) = 1.61, p = .11, η² = 0.04) and ideal age of marriage from 26.9 to 25.8 years (t(55) = 1.82, p = .07, η² = 0.05). The measure of ideal age of first birth would be marginally significant as a one-tailed test while the ideal age of marriage would be significant as a one tailed test (p=0.06 and p=0.04 respectively). These findings are shown in Figure 4.3.
Figure 4.3 Mean (95% confidence intervals) ideal age of first birth and ideal age of marriage.

Dark bars designate warm water condition; light bars designate cold-pressor condition.

There was no significant main effect of condition on desired number of children ($t(63) = 1.50$, ns), discount preference ($t(61) = 1.07$, ns) or global prosocial behaviour ($t(63) = 0.62$, ns). There were also no significant differences between conditions on my measure of desire for companionship with participants no more likely to want to date the male faces I showed them
(t(60) = 0.48, ns), nor quicker to respond to the prompts (t(60) = 0.98, ns). These effects would remain non-significant even under a one-tailed t-test. Descriptive statistics for each dependent measure are reported in Table 4.4

**Table 4.4** Descriptive statistics for variables not significantly different between the warm water and cold-pressor conditions. Data are means (SD) unless otherwise stated.

<table>
<thead>
<tr>
<th></th>
<th>warm water condition</th>
<th>cold-pressor condition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>20.75 (3.92)</td>
<td>20.87 (6.20)</td>
</tr>
<tr>
<td>Contraceptive use (count of women using contraceptives)</td>
<td>19</td>
<td>18</td>
</tr>
<tr>
<td>Menstrual cycle stage (count of women on luteal stage)</td>
<td>19</td>
<td>13</td>
</tr>
<tr>
<td>Desired number of children (0 to 4)</td>
<td>2.47 (1.02)</td>
<td>2.10 (0.98)</td>
</tr>
<tr>
<td>Discount preference (1 to 7)*</td>
<td>4.00 (1.81)</td>
<td>3.52 (1.88)</td>
</tr>
<tr>
<td>Global prosocial behaviour (-6 to 12)**</td>
<td>2.50 (3.37)</td>
<td>2.00 (3.10)</td>
</tr>
<tr>
<td>Responses to male faces (mean number of yes responses) (0 to 0.84)***</td>
<td>0.27 (0.17)</td>
<td>0.29 (0.19)</td>
</tr>
<tr>
<td>Response time to male faces (milliseconds) (937.80 to 2517.24)</td>
<td>1498.14 (314.18)</td>
<td>1599.14 (488.97)</td>
</tr>
</tbody>
</table>

* higher scores indicate a stronger preference for delayed rewards
** higher scores indicate more prosocial behaviour
*** higher scores indicate more positive responses to male faces
Although my findings were only approaching significance for ideal age of first birth and marriage, the change in means due to acute stress for participants’ reported ideal reproductive timing and marriage timing from Study Two are very similar to Study One. Furthermore, I found no evidence that acute stress adjusts women’s ideal ages of first birth and marriage due to a more general shift in their time preference, nor through affecting their desire for companionship.

The finding that my participants did not seem to be seeking social support goes against the theory that in response to stress humans will tend and befriend (Taylor, 2000). This may be because although researchers have investigated the tend-and-befriend pattern in various ways, the only study that I am aware of that has experimentally examined the immediate prosocial tendencies in response to a standardized psychosocial laboratory stressor looked only at male responses (von Dawans et al., 2012). It may also be possible that using how many men an individual desired to date was not an accurate measure of companionship as it might tap into other psychological constructs such as anxiety about dating an unknown individual.

There are mixed findings in the literature on whether acute stress influences time preferences. Individuals under stress make more risky choices (Porcelli & Delgado, 2009), and exogenous cortisol administration increases risk-seeking (Putman, Antypa, Crysovergi, & van der Does, 2010). While these findings point to more risky decision-making under stress, which may translate to shortening time preferences and discounting the future, high basal cortisol levels have actually been associated with less risky behaviour on the Iowa Gambling Task (van Honk, Schutter, Hermans, & Putman, 2003), as well as with lower delay discounting rates (Takahashi, 2004). Furthermore, stress increases risky decision-making in a driving task in older adults, but not in younger adults (Mather, Gorlick, & Lighthall, 2009).
One possible explanation for these conflicting results is that under acute stress, individuals with different levels of exposure to chronic childhood stress might respond differently. For example, individuals exposed to low levels of developmental stress might become more conservative in response to acute stress, whereas individuals exposed to higher levels of developmental stress will respond in more risky patterns to acute stress. This response pattern would be in line with the principles of the life history theory regarding how individuals should adapt their behavioural responses to their environmental conditions. I therefore tested this idea in the following study.

### 4.5 Follow up: Interaction between acute stress and chronic stress

In Study One I looked at the effect of acute stress on female life history strategies, before looking in more depth in Study Two at acute stress and ideal reproductive timing and alternate explanations for females’ adjusted ideals. However, I have not yet looked in depth at how acute stress interacts with females’ previous exposure to chronic stressors, particularly during their childhood development and what effect that interaction may have on their life history strategies and reported ideal age of first birth.

According to the Adaptive Calibration Model of stress responsivity (Del Giudice, et al., 2010), individuals exposed to different levels of stress during development would typically exhibit different levels of stress responsivity. Del Giudice and colleagues propose that individuals exposed to limited childhood stress, characterised by low intensity and infrequent activation of the sympathetic nervous system and hypothalamic-pituitary-adrenal axis during development, are likely to develop a Sensitive stress response phenotype and be highly responsive to stress. Females of this profile would be characterized by a slow life history strategy.
In contrast, individuals exposed to frequent and intense sympathetic nervous system and hypothalamic-pituitary-adrenal axis activation, due to environmental unpredictability and instability during development, would display Vigilant stress response phenotypes. These women are also likely to be highly responsive to stress and on a fast life history trajectory.

Both Sensitive and Vigilant stress response profiles should display high stress responsivity according to the Adaptive Calibration Model; however, I would predict that their different exposures to chronic stress and subsequent life history trajectory might cause individuals to respond to the stress with different behavioural patterns. That is, I predict that females with higher levels of exposure to developmental stress will adjust their ideal reproductive timing to earlier ages relative to females with lower levels of exposure to developmental stress.

4.5.1 Methods

4.5.1.1 Participants

I used data from the 133 female participants (mean age 19.84 years ±3.96) who took part in the cold-pressor experiments reported in Study One and Study Two.

4.5.1.2 Design and procedure

Using data from Study One and Study Two I ran two general linear models to look at the effect of exposure to repeated childhood stressors and the effect of an acute stress response as well as their interaction between each on the significant effects of ideal age of first birth and marriage from Study One and Study Two.
The measure of chronic stress used was the level of early childhood stress experienced by each participant and determined using the 12-item Family Stress Scale (Mikach & Bailey, 1999). Answers to each statement were given on a five-point scale where 1 equalled Strongly Agree and 5 equalled Strongly Disagree. Higher scores indicate a less stressful family situation (Cronbach’s alpha = 0.91). I used the cold-pressor task manipulations from Study One and Study Two as a measure of acute stress.

4.5.2 Results and discussion

There were significant main effects of acute stress \( F(1,120) = 15.57, p < .001, \eta^2 = 0.11 \) and early childhood stress \( F(1,120) = 5.85, p = .02, \eta^2 = 0.04 \) on participants’ reported ideal age of first birth. There were also significant main effects of acute stress \( F(1,120) = 13.54, p < .001, \eta^2 = 0.09 \) and early childhood stress \( F(1,120) = 11.93, p = .001, \eta^2 = 0.08 \) on participants’ reported ideal age of marriage. Furthermore, there was a significant interaction between early childhood and acute stress on ideal age of first birth \( F(1,120) = 4.62, p = .03, \eta^2 = 0.03 \), with the interaction between the main effects approaching significance for ideal age of marriage \( F(1,120) = 2.77, p = .10, \eta^2 = 0.02 \). Results are presented in Table 4.5 and 4.6 and the interaction effects in Figures 4.3 and 4.4.
**Table 4.5** 2x2 analysis of variance for ideal age of marriage by acute stress condition, early childhood stress and their interaction.

<table>
<thead>
<tr>
<th></th>
<th>F</th>
<th>p</th>
<th>η²</th>
</tr>
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<tbody>
<tr>
<td>Intercept</td>
<td>8896.06</td>
<td>&lt;.001</td>
<td></td>
</tr>
<tr>
<td>Acute stress condition</td>
<td>13.54</td>
<td>&lt;.001</td>
<td>0.09</td>
</tr>
<tr>
<td>Early childhood stress</td>
<td>11.93</td>
<td>0.00</td>
<td>0.08</td>
</tr>
<tr>
<td>Interaction</td>
<td>2.77</td>
<td>0.01</td>
<td>0.02</td>
</tr>
</tbody>
</table>

Adjusted $R^2 = 17.8\%$

**Table 4.6** 2x2 analysis of variance for ideal age of first birth by acute stress condition, early childhood stress and their interaction.

<table>
<thead>
<tr>
<th></th>
<th>F</th>
<th>p</th>
<th>η²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>7013.75</td>
<td>&lt;.001</td>
<td></td>
</tr>
<tr>
<td>Acute stress condition</td>
<td>15.57</td>
<td>&lt;.001</td>
<td>0.11</td>
</tr>
<tr>
<td>Early childhood stress</td>
<td>5.85</td>
<td>.02</td>
<td>0.04</td>
</tr>
<tr>
<td>Interaction</td>
<td>4.62</td>
<td>.03</td>
<td>0.03</td>
</tr>
</tbody>
</table>

Adjusted $R^2 = 13.8\%$
Figure 4.4 Mean ideal age of first birth as a function of acute stress condition and early childhood stress. Solid lines represent more experience of early childhood stress. Dashed lines represent less experience of early childhood stress.
Figure 4.5 Mean ideal age of marriage as a function of acute stress condition and early childhood stress. Solid lines represent more experience of early childhood stress. Dashed lines represent less experience of early childhood stress.
The acute stress conditions were further analysed by Bonferroni post hoc tests which were significant ($p < .001$) for both ideal age of first birth ($F(1,120) = 12.65$) and marriage ($F(1,120) = 14.60$). Parameter estimates revealed a significant effect of early childhood stress on ideal age of first birth ($B = 0.60, p = .002$) and marriage ($B = 0.55, p < .001$).

These results show, as predicted, that both acute and early childhood stressors adjust women’s ideal ages of first birth and marriage towards a younger age. Furthermore there is an interaction between these two types of stress. Individuals who reported more exposure to more early childhood stress responded to the acute stress condition by reporting wanting to get married and have children earlier than women exposed to less early childhood stress.

4.6 General discussion

Our findings suggest that both acute and early childhood stress play a part in adjusting female’s reported ideal reproductive timing. I believe this is the first experimental evidence to demonstrate that physiological stress has causal effects on fertility preferences and provides further support for the impact of environmental stress on reproductive timing. My findings suggest that physiological stress may be sufficient to shift women’s preferences towards early reproduction. Repeated exposures to such stressors during development may partly account for the wide socioeconomic variation in age of reproduction within human societies.

Using a laboratory stress paradigm to look at the effect of physiological stress on ideal reproductive timing I showed a significant effect of stress condition on adjusting females’ reported age of first birth and marriage to earlier ideals (Study One). These findings indicate that the cold-pressor caused women to want to get married and have children sooner. In Study Two
I sought to determine whether or not this was a specific effect on reproductive timing or instead a more general effect where female intentions about future reproductive timing are being calibrated through other routes. My results suggest that the acute stress condition did not cause a more general effect on female time preference or desire for companionship.

Finally, in a follow-up study I looked at the interaction between acute and early childhood stress and found that women exposed to higher early childhood stress responded to acute stress by reporting earlier ideal age of first birth and marriage compared with those who were not exposed to as much early childhood stress. These findings are even more striking given that my sample consisted of undergraduate females, who have probably adopted strategies at the slow end of the life history continuum. That is to say, they have invested in continuing their education as opposed to beginning their reproductive careers.

Results from my studies support the large field of literature suggesting that early childhood stress experienced during early development is associated with the direction of an individual’s life history trajectory (Belsky et al., 1991; Belsky, Steinberg, Houts, & Halpern-Felsher, 2010; Chisholm, 1993; Chisholm, 1996; Ellis & Essex, 2007). Furthermore, I provide new experimental evidence that acute physiological stress also has a role to play in regulating female life history strategies, specifically reproductive timing. Although to my knowledge, this has not previously been tested, my findings mirror results from both demographic studies (Cohan & Cole, 2002; Rodgers et al., 2005) and experimental studies (Griskevicius, Delton, Robertson, & Tybur, 2011; Mathews & Sear, 2008) where occurrences or suggestions of mortality have been followed by an increase in the local birth rate, in men’s reported desire to have children and in the acceleration of reproductive ideals.
A question that remains open is how acute stress in the short term might translate to a fast life history strategy in the long term. I do not suppose that my stress manipulation permanently altered my participants’ preferred reproductive timing: it probably returned to normal shortly after the experiment. However, frequent and/or severe exposure to stress, perhaps simply the physiological component, may adjust women’s psychological preferences. An analogy might be the way a spring is extended by a force. Up until its elastic limit, a spring will return to its original length when the force is removed. But after that point, the spring will undergo plastic deformation, and will remain somewhat extended after the force is removed. By analogy, perhaps women’s life history preferences may be elastic until some limit of stress is reached, at which point they become plastic. Individual differences in where that limit is and how they react after the limit may be analogous to the different elastic limits and plastic deformation curves of different materials.

4.7 Limitations and future directions

The findings contribute to the growing field of literature of acute stress and life history strategies that has not as yet been as extensively tested as the effects of early childhood stressors. There are however, a couple of caveats that emphasize the importance of doing further experimental work in this area. First, it is not obvious that a current stressor should reduce the ideal time to first reproduction. Though the matter remains controversial, some evidence suggests that experiences of stress, as reflected by changes in cortisol or follicular phase progesterone, which is similarly secreted by the adrenal gland, reduces current fecundity through increasing the risk of involuntary foetal loss, which would function to delay reproduction (reviewed by Nakamura, Sheps, & Arck, 2008). For example, demographic studies have suggested an increased risk of
stillborns and miscarriages during times of social and economic unrest such as periods of famine (Cai & Feng, 2005).

In cases of severe energetic stress such as famine, I have already argued that resource availability is fundamental to the development of an organism’s life history strategy, and once adequate food and other bio-energetic resources have been taken from the environment to support growth and development other environmental conditions such as morbidity and mortality become important in adjusting life history strategies. The evidence seems to suggest, however, that reproductive failure in humans is not often caused by a single entity event but rather is the result of complex interdependencies of demographic, anamnestic, physiological and psychological risk factors (see Nakamura, et al., 2008). It would be useful for more research to be carried out on stress and maternal health to determine if there is a threshold of stress over which the relationship between reproductive fitness and environmental stress becomes such that adaptive strategies develop to shifting energy away from reproduction and towards survival.

Finally, it is probable that I have mainly tested woman who have adopted strategies at the slow end of the life history continuum. In order to fully assess how acute stress may potentially adjust reproductive timing ideals and to get a clear picture of how this would translate to actual fertility behaviour a larger socioeconomic sample would be useful. In addition, studying populations exposed to higher levels of energetic stress and limited resource availability using this acute physiological stress paradigm might help us understand further why it seems, in some cases, that stress might actually increase foetal loss and potentially delay reproduction.
4.8 Conclusions

Life history theory predicts that selection should favour a point where the costs and benefits of reproductive trade-offs are optimized. Thus, individuals living in conditions of chronic environmental stress who may pay greater costs in delaying childbearing, such as an increased risk of death or becoming incapacitated, should begin to reproduce earlier. While the links between these chronic stressors and reproductive timing have been well studied, less is known about how acute stress may also adjust reproductive timing. I show experimentally that, like early childhood stress, acute stress also calibrates women’s potential reproductive timing. Furthermore, this effect interacts with early childhood stress in a pattern consistent with my understanding of life history strategies and the stress response system such that women exposed to more early childhood stress react to acute stress by shifting the ideals to even earlier ages than those not exposed to early childhood stress. I suggest that attention should be paid to acute stressors as well as chronic stressors to increase the understanding of patterns of early reproduction, such as teenage pregnancy.
Chapter 5

Observed sex ratios and sexual signalling

behavioural change

5.1 Overview

Research into female reproductive timing often involves correlational designs. I adopted similar methodology to explore the variance in female reproductive timing before branching out into experimental and ethological studies. In chapter 3, I explored the psychological mechanisms that predict fertility intentions, exploring how kin networks, mating and reproductive risk taking, discount preference and perceptions of environmental risk predict individual differences in fertility preferences in a socioeconomically diverse sample of adolescents. In a previous study (chapter 2), I used a large data set to explore how the operational sex ratio of a small geographic area predicted the birth rate of a local population. While this approach was correlational in nature it did reveal that the scarcer sex became in greater demand and had a greater influence on subsequent behaviour (female-bias potentially increasing female intrasexual competition and favouring male mating preferences). Another approach, however, is to directly observe human behaviour. This approach is in contrast to the over-reliance on self-reported data and large scale data sets in research exploring reproductive variation. Importantly, such studies may lead researchers to miss important patterns in day to day interactions and individual behaviours that are only
apparent through the direct observation of the specific behaviours of interest. Therefore, in
this chapter I explore the idea that changes in the sex ratio influence female behaviour and
competition using an ethological approach. This study was conducted in order to extend the
understanding of how behaviour changes based on the supply of the opposite sex.

5.2 Introduction

There is a strong tradition of research within the human sciences that aims to explore
predictors of female reproductive timing using large data sets. This research has included
studies linking poor and turbulent early-life conditions, such as parental separation and
frequent residential moves, to early age of first pregnancy in a cohort of British women
(Nettle, Coall, & Dickins, 2011), with similar effects also found in large American (Quinlan,
2003) and Finnish (Pesonen et al. a, 2008) cohorts. Furthermore, research has linked
demographic trends such as female life expectancies (Low, Hazel, Parker, & Welch, 2008),
sex ratios (Chipman & Morrison, 2013) and disease prevalence (Guegan, Thomas,
Hochberg, de Meeûs, & Renaud, 2001) to variations in fertility scheduling and other adaptive
life history strategies across geographic areas ranging from inner city neighbourhoods
(Wilson & Daly, 1997) to cross-cultural analysis (Quinlan, 2007). Even when researchers do
not utilise large, compiled longitudinal and geographical data sets, they must often rely on
questionnaire and survey data of self-reported behaviour (see Nettle and Cockerill, 2010;
Chipman and Morrison, In Press, for examples). In a similar vein, I also used large scale
data sets to explore how the operational sex ratio of a small geographic area predicts the
birth rate of the population (see chapter 2) before turning to questionnaire data to explore the
psychological mechanisms that predict fertility intentions exploring how kin networks, mating
and reproductive risk taking, discount preference, and perceptions of environmental risk predict individual differences in fertility preferences (chapter 3).
These studies are by nature correlational, with stated fertility intentions linked to variables of interest, although there is recent research that attempts to tease apart the causal effects of factors such as stress (Chipman & Morrison, In Press) and sex ratios (Griskevicius et al., 2012) on stated fertility intentions through experimental manipulation. On the one hand, Nettle et al. (2011) have demonstrated that stated fertility intentions can serve as useful proxies for actual reproductive scheduling, when they showed that at the onset of adulthood (age 16), individuals have formed conscious intentions regarding their ideal timing of parenthood and that individuals' intentions were strong predictors of their actual ages of conception and childbearing, even when those events occurred years later. However, the heavy reliance on self-reported data and such questionnaires and surveys—now the dominant method of investigation in human behavioural sciences (Baumeister, Vohs, & Funder, 2007; Furr, 2009) is potentially a cause for concern.

The first problem with psychological research, more generally, is that it often recruits participants from well-off, homogenous samples of university students (Peterson, 2001). Even when data are collected outside of academic institutions, they are from participants who volunteer to take part, leading to issues of participant bias, a clearly identified problem in social science research for decades (Griffith & Walker, 1976). Furthermore, despite the strong link between stated intentions and actual fertility behaviour found in some cases (Nettle et al., 2011) actual behaviour can be substantially different from people’s claims about it, especially if social judgements are attached to certain patterns of behaviour. This leads to problematic questions about the reliability of self-reported data (Garro, 2010). Moreover, an over-reliance on self-reported data and large scale data sets may lead researchers to miss important patterns in day to day interactions and individual behaviours that are only apparent through direct observation of the specific behaviours of interest. Furthermore, people often do not have insight (or have false ideas) about their own behaviour, so there is a need to observe their actual behaviour. Therefore, the aim of this
chapter is to use direct observations to confirm and extend the understanding of behavioural changes based on the supply of the opposite sex.

Previous work has shown a link between operational sex ratios (OSR), the ratio of sexually active males to sexually receptive females, defined in humans as individuals between 15 and 50 years (Lummaa, Merilä, & Kause, 1998), and female fertility scheduling (see Chapter 3). This work is supported by experimental studies that manipulate females’ perception of sex ratios to show that it influences their fertility intentions (Griskevicius et al., 2012).

However, there are two issues with these studies. Firstly, the experimental evidence used women’s stated fertility intentions. Secondly, where research has linked OSR to female fertility scheduling using large scale data sets this research can only analyse behaviour in ultimate terms, i.e. that the adjusting fertility behaviour based on local information about the relative supply of males and females in a locale provides a fitness benefit for the individual. Meanwhile the specific mechanism that precipitates the behavioural calibration can only be guessed at. One potential explanation is that intrasexual competition drives changes in fertility behaviour. This is supported by previous research into animal behaviour. Amongst animal populations, male-biased OSRs result in an increase in male competition, as they must compete more intensively for access to females, which has been shown in the field and in experimental studies (Dick & Elwood, 1996; Krupa & Sih, 1993). At the same time, females become more selective, as there are a greater variety of mates to choose from (Balshine-Earn, 1996). Within populations with female-biased OSRs, the males become more selective due to the greater pool of reproductive partners (Jirotkul, 1999) and in sex-role reversed species, female-female competition increases (Berglund, 1994). For the most part, animal studies of intra-sexual competition have mainly focused on male competition for mates and female mate choice, with female reproductive competition receiving less attention, as it is argued that males usually have higher potential reproductive rates than females and thus have more to gain from being competitive (Clutton-Brock & Parker, 1992). More recently, however, research is emerging on animal behaviour that indicates
intrasexual competition influences not only female mate choice but also direct female-female competition as well, with females not only competing for resources that provide reproductive benefits, but also directly competing for mates, which has led to the evolution of sexual signals analogous to males’ signals (see Stockley and Bro-Jørgensen, 2011 for a thorough review). For example, research has demonstrated that the ornamentation of female birds can signal female quality (Amundsen, 2000), and that females with larger ornaments obtain more sperm from high quality males in some cases (Cornwallis & Birkhead, 2007). The evidence of female sexual signalling in mammals is more ambiguous, suggesting that if females do use signals in competing to attract preferred males, these are most likely to function in advertising fertility and sexual receptivity. The facial colouration of female mandrills Mandrillus sphinx and rhesus macaques Macaca mulatta is brighter during the fertile phase of the oestrous cycle, and the copulatory calls of female baboons Papio also change in relation to oestrous stage, again revealing the most likely time of ovulation, for example (Dubuc et al. 2009; O’Connell & Cowlishaw, 1994; Setchell, Wickings & Knapp, 2006). To my knowledge, however, there has not as yet been any investigation of how sexual signalling behaviours shift based on levels of intrasexual competition.

Flirting behaviours encourage interest from a potential partner, and are therefore one of the first stages of human courtship. Studies investigating different male and female behaviours involved in courtship displays and sexual signalling have, therefore, been conducted (Renninger, Wade & Grammer, 2004; Grammer, Kruck, Juette, & Fink, 2000; Lycett & Dunbar, 1999; Moore, 1985). In contrast to animal studies, the vast majority of human observational studies on sexual signalling have focused on female non-verbal behaviors. Research has found that when soliciting and acknowledging interest in the context of courtship, females are more likely to make the initial non-verbal contact (Givens, 1978) and males are often hesitant to approach a female in the absence of these non-verbal indications of interest (Crook, 1972). These findings make sense in light of the different levels of investment in future offspring between males and females due to sex differences in potential
reproductive rates (Clutton-Brock & Parker, 1992). Men have the potential to reproduce faster, and as a result may have to compete more for mating opportunities. Energy spent providing parental care limits their mating opportunities and their potential reproductive rate. Women on the other hand have lower potential reproductive rates, as mating opportunities may result in a substantial investment of time, energy and resources if a child is conceived. Therefore, females are likely to be the “selectors” and, by proxy, the initiators in the courtship process. Over the last couple of decades, a repertoire of female courtship signals has been established and empirically validated (Grammer, 1990; Kendon & Ferber, 1973; Moore, 1985; Moore, 1995; Moore & Butler, 1989; Scheflen, 1965). Although these studies were conducted in very different settings, from bars to laboratories and during client–therapist interactions, they all observed similarities in the repertoire of female courtship behaviour sexual signals (see below).

Observations of male signals in courtship settings have tended to be focused on indicators of wealth and social status and future competitive success (Lycett & Dunbar, 1999) which are known characteristics that females emphasize in mate choice (Buss et al., 1990; Daly & Wilson, 1983). More recently, however, research has also begun to explore male behaviour and sought to construct a catalogue (see below) of non-verbal courtship signals (Renninger et al., 2004). I sought to use some of the previously observed and established signals to observe whether males and females change or amplify their behaviours based on intrasexual competition as indicated by the operational sex ratio of the focal area.

The goal of the present study was to use an ethological approach to confirm and extend the understanding of how behaviour changes based on the supply of the opposite sex. To do so I examined male and female behaviour and looked for evidence of competition based on the sex ratio of the immediate vicinity in a public, natural setting as part of two exploratory pilot studies. The first pilot was based in bars and pubs in the town centre of Portsmouth, and the second in cafes on the campus of the University of Portsmouth.
5.3 Pilot One: Scanning male and female sexual signals

Our first step in understanding how male and female behaviour might alter based on the sex ratio was to conduct observations of pertinent signalling behaviour in bars and pubs in the town centre of Portsmouth on a weekday evening. I scanned for the following previously catalogued courtship behaviours, six for males and five for females. Measures of male non-verbal behaviour have been adapted from Renninger et al. (2004), and female behaviours from Moore (1985). This analysis is exploratory; however, it is predicted that flirting behaviours will become more common when there is more competition, as the sex that is more common displays more signalling behaviours.

5.3.1 Methods

5.3.1.1 Operational Sex Ratio

OSR is the ratio of sexually active males to sexually receptive females (Kvarnemo & Ahnesjö, 1996). Research from both human and animal studies indicates that the scarcer sex tends to be most in demand and has the greater influence on subsequent behaviour (Chipman & Morrson, 2013). For the purpose of the first pilot the sex ratio of the observational area in the bar was counted every minute in order to determine whether changes in the sex ratio were associated with an increase or decrease in male and female signalling and courtship behaviours. OSR was calculated ratio of males counted in the observation area. OSRs greater than one indicate a male bias.

5.3.1.2 Contact with an unaffiliated female
Observational studies of animal behaviour have shown that populations with male-biased sex ratios have a corresponding increase in male-male competition as males must compete more intensively over a limited pool of females (Dick & Elwood, 1996; Krupa & Sih, 1993). Females also become more selective, as there is a greater variety of mates to choose from (Balshine-Earn, 1996). This would suggest that males would be more successful making contact with an unaffiliated female if the number of females in the focal area outnumbered the number of men. Contact with an unaffiliated female was recorded if a male made conversation contact with a female who was not part of the male’s group at the start of the observation period.

### 5.3.1.3 Male behaviours

#### 5.3.1.3.1 Glancing

De Weerth & Kalma (1995) found that both males and females report eye contact to be the most frequently used courtship-initiation tactic. Therefore, to achieve the necessary eye contact with any surrounding females in order to initiate contact, males need to glance around. Increasing the frequency of their glancing might raise their chances of noticing and attracting female attention. This would suggest that male glancing behaviour might increase as the sex ratio becomes more biased, as males become more competitive in seeking to initiate contact with fewer females. Ethnography of human glancing behaviours in courtship settings has revealed that there are two differentiated types of glancing patterns relevant in courtship settings (Grammer et al., 2000). The first is directed around the room and is sweeping, continuous, and indirect; whereas the second glance is directed towards a target. Within a dark bar setting I chose to focus only on the former type of glance, as targeted glances were subtler and harder to observe successfully. The room-directed glance involved continual head movement occurring concurrently with eye movements. The glancing
movement concludes when an individual under observation returns their head to the position it had been in before the movement was initiated.

5.3.1.3.2 Space maximizing movement

Animal behaviour studies of several social species show that often dominant males like to control larger areas physical space relevant to subordinate males (Alcock, 1993). Likewise, a similar trend has been documented in research into humans' command of their personal and physical space, with more dominant individuals commanding a greater personal radius (Henley, 1977). When observing a courtship setting, males who maximize their personal space through stretching or extending their body to make themselves a larger and more conspicuous target might be more successful at attracting female attention. Males who maximize space might also be signalling to surrounding females that they are more dominant than those around them. High social power is a trait that females have been under evolutionary pressure to value in a mate (Buss, 1989). Thus, I would predict such behaviour to increase as the sex ratio becomes more male-biased. Observations will focus on the male torso area and individuals will be judged to make space maximizing movement when they position their body to take up space greater than the width of their torso. Arms must be extended outside, either on a lateral plane (extending one or both arms or elbows to the side) or on a vertical plane above the head (stretching one or both arms straight upward).

5.3.1.3.3 Closed body movements

In contrast to individuals who maximize their space displaying greater dominance, research has shown that individuals with closed or constricted body position (for example, arms folded across their chest) are perceived as having less social power (Archer, 1980; Goffman, 1961). Males who constrict their body movement should, therefore, have less success attracting female attention. Closed body movements would be predicted to decrease in
response to male-biased sex ratios. Participants will be recorded as making a closed body movement when their arms are positioned so that their upper body and torso are covered from view. This will include positions such as limbs crossed on chest, a hand gripping the opposite shoulder, or sustained touching of an object so that the limb obstructs the view of the torso.

5.3.1.3.4 Non-reciprocated touches

Research on touching behaviour has found that different patterns provide indications for observers about the relative social status of the group members (Grammer et al., 2000). While reciprocated touches are often perceived by observers to indicate affection or empathy (Summerhayes & Suchner, 1978), non-reciprocated touches are often perceived as dominant, or indicating social status (Burgoon, 1991). Individuals directing their touches to other group members are judged to have higher status and more social power than those individuals who only receive touches. Therefore, males who make more non-reciprocated touches should be more successful with females and such behaviour might increase, as there are fewer available females. Non-reciprocated touches are defined as the administration of intentional body contact from one male to another individual where the targeted individual does not return bodily contact to the initiator. Touches might include a brief tap or an extended rest of a limb of the touch initiator on the target individual.

5.3.1.3.5 Self-directed touches

Self-directed touches, or automanipulations, include behaviours such as rubbing the face, scratching, or playing with one's hair and are often conceptualized as "displacement-like activities" (Givens, 1978). Such displacement-like activities are theorized as a pattern of
behaviour where the tension from an organism’s motivation (in a courtship context, such tension might be a result of the desire to initiate contact or fear of initiating contact, etc.) is replaced by a secondary activity (Harrison, 1965). In the courtship rituals of many species, automanipulations become exaggerated and display-oriented, communicating information about the general motivational state of the organism (Dilger, 1962, McKinney, 1965). In humans, displacement activities may serve as covert attention signals. In males, increasing self-directed touches towards the head may highlight the jaw/beard-growth area, drawing females’ attention to facial indicators of their secondary sexual characteristics and potentially emphasizing their masculinity. On the other hand, however, there is also abundant literature that self-directed touches are associated with stress (Castle, Whiten, & Aureli, 1999). Furthermore, there is some evidence that displacement behaviour such as self-directed touches lower stress levels in men (Mohiyeddini, Bauer, & Semple, 2013). Therefore, men in environments with a male-bias in the sex ratio might also increase self-directed touches to lower stress levels in environments that have potential for increased male-male competition.

Self-directed touches were recorded when an individual made movements of the hand into contact with part of their own face, neck or hair.

5.3.1.4. Female behaviours

5.3.1.4.1 Glancing

Just as with males, glancing is an important behaviour for females wishing to initiate courtship (de Weerth & Kalma, 1995). Cary (1976) shows that it is women’s glancing behaviour that is important in initiating conversation between strangers. Both in laboratory settings and in natural settings, such as bars and clubs, conversation was initiated only after the woman glanced at the man more than once. Therefore, females who increase the frequency of their glances might raise the probability that they will notice and attract
interested males. Glancing may also increase competitively as intrasexual competition increases as indicated by a female-biased sex ratio. Observations have recorded the importance of the “coy glance” (eye contact followed by immediate eye aversion) signalling female interest and resulting in an approach and/or the maintained interest of the target (Moore, 1985; Eibl-Eibesfeldt, 1971). However, targeted glances are subtle and harder to observe successfully, especially a movement as rapid as eye contact with immediate eye aversion. Therefore, observing glancing behaviour was restricted to sweeping and continuous room-wide glancing.

5.3.1.4.2 Male directed smiling

Researchers found that once women caught the eye of a man, a targeted smile was a common courtship signal (Eibl-Eibesfeldt, 1971). Male directed smiling can signal female interest (Grammer, 1990) and serve as an important stepping stone from initial eye contact towards creating a greater sense of intimacy. Researchers observing human courtship behaviour often find mutual gazing and smiling followed by proximity and touching behaviours, with partners reaching synchrony in gesture and movement (Argyle, 2013; Maxwell, Cook, & Burr, 1985). Grammer, Kruck, and Magnusson (1998) found evidence of female manipulation of males in a non-intrusive and non-obvious way through the use of body movement and smiling. In addition, smiling faces have been repeatedly rated as being more physically attractive than neutral ones (Mehu, 2006). This could potentially mean that males would glance longer at a female who is smiling towards them. Although it might be difficult to accurately observe such behaviours, recording female signalling in terms of male directed smiles might serve as a middle ground between the more generalized room encompassing glances and the more exaggerated behaviour also described here and used in observation in the pilot study. I predict that if female-biased OSRs increase female-female competition, then more male directed smiling behaviour would be observed in such
conditions. A male directed smile was recorded if a female’s mouth turned upwards while she was looking directly at a focal male. Smiling behaviour was often accompanied by leaning closer and touching the focal male.

5.3.1.4.3 Laughing behaviour

As with coy gaze patterns, researchers have identified females coyly smiling at a male target as a reliable courtship signal (Moore, 1985). Observations have focused on female laughing behaviour in addition to male directed smiling, as it is thought that coy smiles might be difficult to observe and identify reliably. Laughter has also been observed to be a behaviour commonly used in female courtship signalling (Moore, 1995). Research on laughter indicates that it is often a ritualized behaviour signalling submission and communicating female interest in the male (Grammer, 1990). Laughter also has a social bonding function, which emerges in intersexual encounters such as courtship, i.e. the signalling of interest in a partner takes place (Grammer & Eibl-Eibesfeldt, 1990). Furthermore, laughter may be more effective in attracting attention from surrounding males than a coy smile; especially in settings where more females are competing for attention. Behaviour is recorded as laughing when a relaxed, open mouth display is observed, with or without vocalizations audible to the researchers.

5.3.1.4.4 Space maximizing movements

Considerable research indicates that an important cue of female physical attractiveness is breast size and a low waist-to-hip ratio (i.e. a more curvaceous body) (Singh & Young, 1995; Tovée, Maisey, Emery, & Cornelissen, 1999; Weeden & Sabini, 2005). An erect and open posture has also been observed as a successful female courtship tactic (Argyle, 2013). In a
competitive courtship setting therefore, a female stretching and extending her upper body might not only be making herself a larger and more conspicuous target, and thus attracting male attention, but also be making her breast area more conspicuous to the opposite sex. I would predict such behaviours to increase as the sex ratio becomes more female-biased increasing the intrasexual competition.

5.3.1.4.5 Self-directed touches

Preening behaviour is another commonly observed behaviour in human females when courting and signalling attraction (Kendon & Ferber, 1973; Moore, 1985; Moore, 1995). This preening behaviour might serve the same function as self-directed touch in males, where motivational tensions arise and are replaced by a secondary activity such as fixing the hair or touching the face. These behaviours might even be exaggerated and display-oriented, communicating a desire to be approached and initiate contact, acting as covert attention signals. Female self-directed touching behaviour should increase as the sex ratio becomes more female-biased.

5.3.2 Procedure

Seven hours of observations were conducted over four evenings (6-8pm) on Wednesday and Thursday nights, close to the university in three bars in the Palmerston Rd and Guildhall areas of Portsmouth. These bars contain seating areas of similar sizes, a relatively constant crowd and an unobstructed view of the room. At the beginning of each 30 minute observation period, another researcher (Z.K.) and I completed a scan sample of the number of men and women in the observation area and scanned the bar area for the focal male and female behaviours at 20 second intervals. After one minute, we counted the number of men
and women in the observation area and then repeated scanning for male and female
behaviour at 20 second intervals. This minute long cycle continued for the duration of the 30
minute observation period.

Observations were conducted by two of us to ensure inter-observer reliability. This was
calculated for three and a half hours of observation using the following formula: \[\frac{\text{Number of agreements (A+B)}}{\text{Number of agreements (A+B)}} + \text{Number seen by A only} + \text{Number seen by B only}] \text{ (McGrew, 1972). Only self-directed male touches had an inter-observer reliability less than .50 and this signal was excluded from further analysis. The range of inter-observer reliability scores for the remaining 11 male and female behaviours and the OSR was .52–.95, with the average score equalling .70. Inter-observer reliability scores are found in Table 5.1.}
Table 5.1 Descriptive statistics (range, means and SDs) and inter-observer reliability scores for observed male and female behaviours and the sex ratio for the first pilot study.

<table>
<thead>
<tr>
<th></th>
<th>Range</th>
<th>Mean (SD)</th>
<th>Inter-observer reliability</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Sex ratio</strong></td>
<td>0.09–25</td>
<td>3.28 (4.19)</td>
<td></td>
</tr>
<tr>
<td><strong>Contact with female</strong></td>
<td>0–1.33</td>
<td>.06 (.18)</td>
<td>0.80</td>
</tr>
<tr>
<td><strong>Male behaviours</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glancing</td>
<td>0–1</td>
<td>.09 (.16)</td>
<td>0.52</td>
</tr>
<tr>
<td>Space maximizing</td>
<td>0–1.33</td>
<td>.06 (1.3)</td>
<td>0.65</td>
</tr>
<tr>
<td>Closed body movements</td>
<td>0–.80</td>
<td>.05 (.12)</td>
<td>0.60</td>
</tr>
<tr>
<td>Non-reciprocated touches</td>
<td>0–.5</td>
<td>.01 (.05)</td>
<td>0.90</td>
</tr>
<tr>
<td>Self-directed touches</td>
<td>0–1</td>
<td>.09 (.15)</td>
<td>0.44</td>
</tr>
<tr>
<td><strong>Female behaviours</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glancing</td>
<td>0–1</td>
<td>.05 (.13)</td>
<td>0.73</td>
</tr>
<tr>
<td>Space maximizing</td>
<td>0–.67</td>
<td>.01 (.07)</td>
<td>0.95</td>
</tr>
<tr>
<td>Male directed smiling</td>
<td>0–2</td>
<td>.10 (.21)</td>
<td>0.59</td>
</tr>
<tr>
<td>Laughing</td>
<td>0–1</td>
<td>.03 (.13)</td>
<td>0.95</td>
</tr>
<tr>
<td>Self-directed touches</td>
<td>0–1.50</td>
<td>.11 (.20)</td>
<td>0.60</td>
</tr>
</tbody>
</table>

* Higher scores indicate male biased sex ratios (observations per minute)
** Higher scores indicate increase in the observed behaviour (observations per minute treated as a proportion of the number of males in the observational area)
*** Higher scores indicate increase in the observed behaviour (observations per minute treated as a proportion of the number of females in the observational area)

A series of bivariate correlations were computed in SPSS Version 20 to determine the relationship between the OSR of the observational area and five male and five female behaviours. The ten behaviours were also compared to a median split of OSR, turning OSR as a continuous variable into a categorical variable (high OSR= male bias, low OSR= female bias). Finally, a composite score was created for both male and female behaviour. This measure was the sum of the individual male and female signalling behaviours (forming the
Male and Female Composite score respectively). The composite measures were compared to the OSR and OSR median split.

All individuals observed were in public spaces where they would have expected their behaviour to be visible to others. No personally identifying information was recorded, and, although I was never questioned, I was ready to explain the nature and purpose of the study to any individual concerned. The study was approved by the Department of Psychology, Ethics Committee, University of Portsmouth.

5.3.3 Results & discussion

Descriptive statistics for the observed behaviour and OSR are found in Table 1. When comparing male and female behaviour to the sex ratio of the observational area, as the observational area became more male-biased, there was less frequent contact with unaffiliated females ($r = -0.17, p = .02$) and males also glanced around the bar less frequently ($r = -0.21, p = .002$). Male glancing behaviour was also significantly associated with the OSR median split ($r = -0.26, p < .001$), with male-biased OSRs moderately correlated with less glancing. Contact with unaffiliated females was approaching a significant association with the OSR split ($r = -0.12, p = .09$).

For females, male directed smiling behaviour was associated with the OSR split ($r = 0.16, p = .02$). Female-biased OSRs were moderately correlated to a higher proportion of females smiling at targeted males.

Finally, I found that the composite suite (total signalling behaviours) of male behaviours was significantly associated with the OSR split ($r = -0.21 p = .002$). As the environment became more male-biased, male signalling behaviour was observed to decrease. Likewise, the composite suite of female behaviours was significantly associated with the OSR split ($r =
0.18, \( p = .01 \). As the observational area became more female-biased, female signalling behaviour was observed to increase. Results are found in Table 5.2.

Table 5.2 Significant correlations in pilot study one between the sex ratio and observed behaviours.

<table>
<thead>
<tr>
<th></th>
<th>Sex Ratio</th>
<th>Sex Ratio Split</th>
</tr>
</thead>
<tbody>
<tr>
<td>Contact with females</td>
<td>-0.17**</td>
<td>-0.12*</td>
</tr>
<tr>
<td><strong>Male behaviours</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glancing</td>
<td>-0.21***</td>
<td>-0.26***</td>
</tr>
<tr>
<td>Space maximizing movements</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Closed body movements</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Non-reciprocated touches</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Composite male behaviour</td>
<td>ns</td>
<td>-0.21***</td>
</tr>
<tr>
<td><strong>Female behaviours</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glancing</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Space maximising movements</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Male directed smiling</td>
<td>ns</td>
<td>0.16**</td>
</tr>
<tr>
<td>Laughing</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Self-directed touches</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Composite female behaviour</td>
<td>ns</td>
<td>0.18**</td>
</tr>
</tbody>
</table>

* \( p < .1 \)

** \( p < .5 \)

*** \( p < .005 \)
Overall, as predicted, the suite of female signals increased in locations with higher female competition. Individually, female smiling behaviour also increased in more female crowded and potentially competitive environments. Interestingly, however, the suite of overall male signalling behaviours and individual male behaviours of glancing and contact with an unaffiliated female decreased in more male-biased environments.

However, the literature on both observational and interview studies indicate that solicitation in courtship interactions is mainly done through the female’s non-verbal messages (Grammer, et al., 2000; Renninger et al., 2004). Therefore, in order to attract attention, females must send more signals in a highly competitive environment. Indeed, Moore & Butler (1989) conclude that the frequency of female signalling is the most important factor in determining approaches from men. A high-signalling woman, of average attractiveness, is more likely to be approached than a low-signalling, beautiful woman.

These findings make sense in light of the differential potential reproductive rates (Clutton-Brock & Parker, 1992). My findings for female behaviour seem to indicate that females need to send more signals under intense competition, when there are fewer available males.

This finding, coupled with the fact that studies on OSRs indicate that the scarcer sex tends to be most in demand and has the greater influence on subsequent behaviour (Chipman & Morrison, 2013), may potentially explain the decrease in male signalling in male-biased OSRs. Because females are the selectors in courtship settings, males are therefore less likely to be successful in male-biased environments (initiate less contact with unaffiliated females) and so expend less effort to attract female attention (limit glancing behaviours). An increase in male glancing \((r = 0.38, p < .001)\) and male space maximizing \((r = 0.23, p=.001)\) was associated with an increase in contact with an unaffiliated female. Perhaps this suggests that when the opportunity does present itself, men increase their signalling behaviours to facilitate their chance of receiving the necessary signals from the female.
There are however, a number of crucial limitations of my data that make inferences based on my results restricted at best. Firstly, most of the signalling behaviours observed did not change based on the sex ratio of the observational area, despite using extensively catalogued male and female courtship behaviours in my study. However, the composite scores did indicate that the measures observed did, in part, capture relevant signalling behaviour as composite measures of male and female behaviour were linked to the sex ratio. For the most part, however, the behaviours observed are fairly constant in courtship contexts, and there are other relevant signals that respond more sensitively to cues of intrasexual competition. Or it may be that the sex ratio of an area bar does not provide an appropriate level of competition. The sex ratio of a social group that has gone to the bar together may provide a more suitable level of local intrasexual competition.

Secondly, and more seriously, my scan sample observational design means that I cannot discount pseudoreplication of the data as driving my results. Because of the nature of the observational area, with many individuals moving around, I could not attribute behaviours to specific individuals. This could result in a sampling error as a result of extracting more than a single data point per individual, then simply adding these data to the main data set. Thus the data points in the sample are not independent, without using an appropriate repeated measures statistical technique. This results in an artificially inflated sample size, which falsely raises statistical power and increases the chances of making a type I error (Waller, Warmelink, Liebal, Micheletta, Slocombe, 2013). See Hurlbert (1984) and Machlis, Dodd, & Fentress, (1985) for an extensive discussion of the issue of pseudoreplication in ecological field experiments. Essentially pseudoreplication distorts the purpose of data gathering in ethological studies from obtaining large behavioural samples as opposed to collecting samples of behaviour from a large number of individuals. As a result, the risk of Type 1 error (i.e. rejecting a true null hypothesis) is much greater and the true alpha level is either much higher or much lower than the conventional 0.05. Therefore, the interpretation of any
statistical analysis that does not control for, or remove, pseudoreplication, becomes unsound.

5.4 Pilot Two: Focusing on group male and female sexual signals

Due to the serious limitations of the first pilot study, my second step was to create an observational design that removed the risk of pseudoreplication. I therefore observed a focal group, comprised of 4 or 5 group members, in order to record each group member’s behaviour and to judge if their behaviour changed in response to differences in the sex ratio of the group. This had the added benefit of determining whether the sex ratio of a group was a better indicator of behavioural adjustments in response to local intrasexual competition, as the first pilot had not revealed many differences in signalling behaviours based on the sex ratio of the observational area. The observations of pertinent signalling behaviour were done in cafes on the university campus in Portsmouth during week days. I continued to utilize the signalling behaviours from the first pilot, as these behaviours were catalogued as reliable courtship signals (Renninger et al., 2004). However, the same five signals were scored for both males and females for ease of coding and to minimize the changes between each pilot study. This approach should remove pseudoreplication of the data from the current pilot as well as determine whether group OSR was a better predictor of competition, as judged by shifting male and female courtship and signalling behaviours.

5.4.1 Methods

5.4.1.1 Measures

As both the male and female behaviour observed in the pilot has previously been catalogued as reliable sexual signalling in courtship contexts in previous observational studies (e.g.
Renninger et al., 2004; Moore, 1985), and to limit changes to the observed signalling behaviour between pilot studies, I continued to observe the same catalogue of signalling behaviours in the second pilot study. As the scanning technique was now focal I limited this pilot study to recording the male signalling behaviours observed in pilot study one. I would expect glancing behaviour, space maximizing movements, automanipulations and non-reciprocated touches amongst both male and females to increase as intrasexual competition increased. Closed body movements, however, would be expected to decrease as intrasexual competition increased.

5.4.1.2 Procedure

Fifty focal groups and a total of 172 individuals were observed over a total of seven and a half hours, conducted over four days (10-1pm) on Wednesday and Thursday in two cafes on the campus of the University of Portsmouth. These cafes contained seating areas of similar sizes, a relatively constant crowd and an unobstructed view of the room. At the beginning of each observation period I scanned for a group containing exactly four or five group members. The scanning technique was instantaneous at 10 second intervals. I then recorded the number of males and the number of females in the focal group and began to record signalling behaviour for the duration of the observation period. Observation periods lasted from three to fifteen minutes and would finish when one group member or the whole group moved, or other individuals joined the focal group.

Observations were carried out by a single researcher. However, the behaviour observed was clear and unambiguous and there had previously been no problem with observer reliability in the first pilot study. Only non-reciprocated touches fell below the acceptable threshold (McGrew, 1972). However, non-reciprocated touches were more clear and unambiguous in a cafe compared with a bar and were therefore retained for observation.
As the data were nonparametric, a series of Spearman’s correlations were computed in SPSS Version 20 to determine the relationship between the OSR of the focal group and the five observed behaviours proportional to the time each group was observed. The observed behaviours were also compared to the OSR split. Secondly, the data were log transformed and analysed using a generalized linear mixed model (GLMM) with individuals (level one) nested in focal group (level two). I also created a binary logistic regression and looked at the OSR in relation to the presence or absence of the five observed behaviours. Finally, I looked at male and female behaviours separately in relation to the OSR and the OSR split.

All individuals observed were in public spaces where they would have expected their behaviour to be visible to others. No personally identifying information was recorded, and the researcher, though never questioned, was ready to explain the nature and purpose of the study to any individual concerned. The study was approved by the Department of Psychology, Ethics Committee, University of Portsmouth.

5.4.2 Results & Discussion

Descriptive statistics for the observed behaviour and OSR are found in Table 5.3. There were no significant correlations between the five observed behaviours and the OSR or the OSR split. There were also no significant results from the GLMM or the binary logistic regression. Observing male behaviours on their own revealed no significant results, only for female behaviours did the rate of non-reciprocated touches approach a significant association with the sex ratio of the focal group ($r = 0.64$, $p = .07$) as the sex ratio became more male-biased, females increased intentional body contact from one individual to another.


### Table 5.3

Descriptive statistics (range, means and SDs) for observed male and female behaviours and the sex ratio for the second pilot study.

<table>
<thead>
<tr>
<th></th>
<th>Range</th>
<th>Mean (SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex ratio</td>
<td>0-1</td>
<td>0.47</td>
</tr>
<tr>
<td>Glancing</td>
<td>0-.71</td>
<td>0.26 (.20)</td>
</tr>
<tr>
<td>Space maximising movements</td>
<td>0-1.80</td>
<td>0.33 (.30)</td>
</tr>
<tr>
<td>Self-directed touches</td>
<td>0-2.50</td>
<td>0.38 (.40)</td>
</tr>
<tr>
<td>Closed body movements</td>
<td>0-1</td>
<td>0.28 (.27)</td>
</tr>
<tr>
<td>Non-reciprocated touches</td>
<td>.10-.10</td>
<td>0.10 (00)</td>
</tr>
</tbody>
</table>

* Higher scores indicate male biased sex ratios (observations per minute)

** Higher scores indicate increase in the observed behaviour (observations per minute)

As with the first pilot, however, there are a number of limitations of my data. The first was that the power of the second study was very low. There were only 9 cases of non-reciprocated touches and, at most, 76 automanipulations. Secondly, a cafe in the middle of the day was potentially not the right context to observe courtship and signalling behaviours. Moore (1985) found women were more likely to display higher frequencies of non-verbal sexual signalling when in what she called “mate relevant” contexts such as singles’ bars, in contrast to a university snack bar. In addition to the context not being right for observing non-verbal courtship behaviours, it is also possible that it was the wrong level at which to make inferences about how the sex ratio manipulates behaviour: most likely individuals sat with friends and individuals with whom they were unlikely to engage romantically. Perhaps the sex ratio of the entire cafe would have had more sway on signalling behaviour, although there is still likely to be more signalling in a bar in the evening than in a cafe in the daytime. Finally, as with the first pilot I am unable to discount the possibility that there are other relevant signals that respond more sensitively to cues of intrasexual competition.
5.5 General Discussion

Despite the limitations of both pilot studies, understanding how intrasexual competition influences and predicts sexual signalling is a crucial step in completing my understanding of how the intrasexual competition is linked both to human mating preferences and human fertility scheduling.

There is also considerable scope to add to the understanding of male and female sex differences in sexual signalling if such a study is done correctly. The majority of human and animal studies seem to suggest that what is important, when there are high levels of intrasexual competition, is male signalling and female mate choice (e.g. Krupa & Sih, 1993; Balshine-Earn, 1996, Renninger et al., 2004). Yet, new evidence has begun to emerge that female competition is associated with many diverse adaptations including conspicuous sexual signals (Amundsen, 2000). However, animal behaviour research also seems to indicate that female adaptations for intrasexual competition are often less conspicuous than those of males, most likely for reasons relating to higher female parental investment and lower potential reproductive rates (Clutton-Brock & Parker, 1992). Overt displays of female reproductive competition may be less persistently expressed, making them difficult to observe (Carranza, Alarcos, Sanchez-Prieto, Valencia, & Mateos, 2004). Likewise, evidence of direct female-female competition in humans is also not clear and the studies that have been conducted seem to suggest that female intrasexual competition is most likely to influence female sexual signalling when they are on the fertile stage of their menstrual cycle. For example Haselton, Mortezaie, Pillsworth, Bleske-Rechek, & Frederick (2007) found that women changed their self-grooming and ornamentation (choosing more attractive and more revealing dresses) the closer they were to ovulation.

There were a number of practical difficulties with the observational sampling. For example, behaviours were often subtle and I felt that I could be missing signals. Secondly, conducting the research in a bar was probably more likely to reveal observations of flirting behaviour
than in a café. However, due to ethical constraints and without the availability of a research assistant I was unable to conduct the second pilot study in a similar location to the first pilot. While challenging, observational methodology is under-used in human studies and worth pursuing. Greater time must be spent on developing a more complete catalogue of human traits likely to be influenced by changes in the rate of intrasexual competition including non-verbal behaviours and ornamentation. There are also a great deal more experimental work conducted than ethological studies of how people actually communicate and signal. Studies should also be confined to mate relevant contexts and the OSR of the larger area and the immediate focal group should also be recorded to see which holds greater sway over behaviour in a mate relevant context and whether the two OSRs interact in a way that has new insights for human intrasexual competition and sexual signalling.
Chapter 6

General discussion

6.1 Overview

Throughout this thesis I have focused on several main themes: 1) the impact of sex ratios on reproductive and behavioural variation, 2) the importance of subjective perceptions of the environment on fertility intentions, 3) how individuals' propensity towards risk taking and knowledge of safe sexual practice suggest individuals respond adaptively based on their fertility intentions, 4) how kin networks shape life history strategies, and 5) how a causal exploration of acute stress and its interaction with chronic stress can inform the understanding of individual variation in ideal reproductive timing in new ways. Combined, the resulting studies contribute to an integrated understanding of adaptive human behavioural flexibility. Firstly, I demonstrate that the impacts of social and environmental stressors such as the local sex ratio result in different response patterns from women with different socioeconomic backgrounds, the implication being that women with different life history trajectories have different strategic responses to environmental conditions in line with the predictions of life history theory. Secondly, I show that individuals' subjective perceptions of their environment are just as important, and potentially more important, indicators of their fertility intentions than the often used objective indicators of environment quality such as deprivation. Thirdly, I show that individuals take risks in strategic ways that can be explained
by evolutionary principles and that their future reproductive intentions are supported by prenatal norms and are not due to deficiencies in their knowledge of safe sexual practice.

Fourthly, I consider the evidence that kin networks help shape individuals' life history strategies. Finally, I explore the causal pathways by which acute stress shifts individuals' life history strategies and how this adjustment is moderated by an individual’s exposure to chronic childhood stressors. Overall, the results demonstrate the utility of a multi-methodological approach to the study of human reproductive variation and behavioural flexibility. This thesis has been productive, albeit with some challenges, and highlights the need to conduct further studies; in particular, those which aim to understand the strategic behavioural variation of individuals from a broad socioeconomic spectrum with different exposures to chronic stress and on different life history trajectories. This thesis has implications for future policy aimed at reducing the rate of teenage pregnancy and also moves towards an integration of the proximate and ultimate mechanisms in understanding human reproductive variation.

6.2 Summary of main findings and implications

6.2.1 Sex ratios and behavioural variation

Research on childbearing has identified a strong relationship between environmental conditions, such as local levels of deprivation and reproductive variation (Nettle, 2010). In Chapter 2, I showed that in addition to the well-established effect of deprivation, differences in the sex ratio of an environment also predict changes to the local birth rate. I demonstrated that female-biased populations predict early reproduction in the most deprived wards. This effect reverses at older ages, so that, from the age of 30, in the least deprived wards, female-biased sex ratios predicted higher birth rates. I interpreted this finding as being due to female-female competition or limited mate choice, such that, as the chance of attracting a
high-investing partner is reduced in female-biased wards, women from deprived areas calibrate towards the fast end of the life history continuum. Thus they begin to reproduce earlier, boosting early reproduction in these areas. By contrast, women from less deprived areas with slow life history characteristics adopt the opposite strategies in response to female-biased sex ratios, and delay reproduction. This would suggest that the interaction between deprivation and sex ratios is vital to understanding individual adjustments to fertility schedules. This interaction between the immediately relevant environmental conditions (supply of a potential mate) and long term environmental conditions (deprivation) would go on to inform my experimental work in Chapter 4 where I explored the interaction between acute stress (an immediately relevant environmental condition) and chronic stress (a long term environmental condition).

In addition, this finding suggests that individuals are monitoring their local ecologies for the supply of one sex to the other, which may be related to reproductive behaviour that accounted for the results. Previous research has already shown that individuals monitor for perceived environmental risks (Johns, 2011) which I explore further in Chapter 3.

As the findings on sex ratios, economic status and local birth presented in Chapter 2 linked OSRs to female fertility scheduling using large scale data sets, this study could only analyze behaviour in ultimate terms. That is, while the data suggest that there are adjustments to fertility behaviour based on local information about the relative supply of males and females in a local environment which provides fitness benefits for the individual, the specific mechanisms that precipitate that calibration can only be hypothesised.

My interpretation of the result, however, was that intrasexual competition potentially drives changes in fertility behaviour. Therefore, I also conducted a study using an ethological approach to confirm and extend the understanding of how human flirting behaviour changes based on the supply of the opposite sex, the results of which are presented in Chapter 5. To
do so, I examined male and female behaviour and looked for evidence of competition based on the sex ratio of the immediate vicinity in a public, natural setting as part of two exploratory pilot studies. However, in the first pilot, my scan sample observational design means that I cannot discount pseudoreplication of the data as driving my results. Because of the nature of the observational area, with many individuals moving around, I could not attribute behaviours to specific individuals. In an effort to correct this limitation, I observed a focal group, comprised of 4 or 5 group members, in order to record each group member’s behaviour and to judge if their behaviour changed in response to differences in the sex ratio of the group. However, the setting of the pilot study was relocated from a pub to a cafe in the middle of the day. This environment was potentially not the right context to observe courtship and signalling behaviours. Likewise, I found much lower frequencies of sexual signalling, and as a consequence had no significant findings.

I do, however, believe that there is potential to add to the understanding of male and female sex differences in sexual signalling using improved observational methodology. Female adaptations for intrasexual competition may be less conspicuous than those of males and clear displays of female reproductive competition may be less persistently expressed than male-male competition making them difficult to observe (Carranza, Alarcos, Sanchez-Prieto, Valencia, & Mateos, 2004). It may, therefore, be more fruitful to focus on observations of male signals in courtship settings, such as those indicators of wealth, social status and future competitive success which are known characteristics that females emphasize in mate choice (Buss et al., 1990; Daly & Wilson, 1983). In short, focusing on male conspicuous consumption (e.g. buying drinks for others in a pub) and then observing success in contacting unaffiliated females might yield interesting findings.
6.2.2 Subjective perceptions of the environment

In Chapter 3, my results indicated that adolescents’ subjective perceptions of environmental risk were important predictors of their fertility intentions. I found that the adolescents in my study who had shorter perceived life expectancies favoured earlier reproduction. My interpretation of this finding is that individuals are potentially able to monitor the mortality risk of their environments by means of their subjective life expectancy, and are adjusting their ideal age of first birth accordingly. This result suggests that perceptions of mortality threats are as salient as perceptions of more general environmental risk, which also predicted adolescents’ ideal reproductive timing.

In contrast, objective measures of environment quality, such as local levels of deprivation, did not significantly alter adolescents’ fertility intentions in my model, nor did the adolescents’ socioeconomic status. My results show the importance of accounting for individuals’ perceptions of their environment, and not only objective measures of deprivation, when examining early childbearing and differences in fertility intentions. This concurs with Johns (2011) and Upchurch, Aneshensal, Sucoff and Levy-Storms (1999) who demonstrated that experiential neighbourhood perceptions were as important in predicting adolescent sexual activity as structural neighbourhood components.

Less perceived environmental and school risk also predicted adolescents reporting a greater number of desired offspring. This suggests that the participants want fewer offspring when they perceive their environment to be uncertain and unsafe. This association was stronger for female adolescents. On the other hand, previous research has been conducted on mortality salience and the desire for offspring which found that individuals primed to think about their own mortality reported wanting more children. While an individual’s perception of their own mortality was not a significant predictor of wanting more offspring there was a significant sex by subjective life expectancy interaction with the association stronger for male
adolescents. Other studies examining mortality salience and desired offspring in particular, have found the association strong for males not females (Mathews & Sear, 2008). My findings, along with previous research, potentially point to different associations between a desire for offspring and perceptions of general environmental quality and perceptions of mortality. My findings also potentially suggest an important sex difference in light of these perceptions in terms of increasing individuals’ desires to procreate. This is an area where further research is needed.

Not all results, however, were in the expected direction. Interestingly, school risk was also significantly associated with ideal age of first birth but in the opposite direction to that predicted, with an increase in perceived school risk predicting later reproduction. This may be because, unlike an individual’s home environment, schools are largely a chosen environment after the age of 16 in the United Kingdom. Perceived school risk might be a more salient predictor of fertility intentions at younger ages, as individuals who view their school environment negatively might be more likely to drop out and pursue childbearing as an alternative to educational attainment (Fergusson & Woodward, 2000). Furthermore, the attitudes taught directly or indirectly (from peers) in schools, might be a better indicator of subsequent developing ideas on reproductive behaviour and attitudes. Previous research has shown that school level characteristics are associated with individual behaviours, such as age of first intercourse (Bearman & Brückner, 2001).

6.2.3 Propensity towards risk taking and knowledge of safe sexual practice

The results of my questionnaire study presented in Chapter 3 showed that adolescents’ propensity towards risk taking is also potentially strategically adaptive. Adolescents who wanted more offspring reported being less likely to take reproductive risks and also viewed
such behaviours as more risky. There was also a significant sex by perceived reproductive risk interaction, with the association stronger for female adolescents. As women have limited reproductive careers and successful reproduction represents a substantial investment, it would be rational for a woman, compared to the opposite sex, to limit the reproductive risks she exposes herself to, so that she has an opportunity to have the number of offspring she desires within a relatively limited time frame.

Adolescents with a later ideal age of first birth report a greater likelihood of taking reproductive risks than their peers in my study. However, there was no difference in perceived riskiness, suggesting that these individuals recognize the risk inherent in their behaviour. These findings suggest that adolescents in my sample who were less interested in reproducing were more likely to take reproductive risks. Perhaps they were less concerned with the potential impact such risks would have on their reproductive potential. Adolescents who want a greater number of children also view items on the mating risk taking scale as less risky. This could indicate more willingness to engage in sexual activity, or stronger pro-natal norms associated with their desire for offspring.

Subjective knowledge of safe sexual practice (indicating stronger pro-natal and anti-contraception use norms), as opposed to objective knowledge of safe sexual practice (indicating factual knowledge of safe sexual practice), predict adolescents in my sample reporting a desire to have more offspring. There was also a significant sex by subjective knowledge of safe sexual practice interaction associated with reproductive timing. Male adolescents with higher scores on subjective knowledge of safe sexual practice have an earlier ideal age of first birth. These findings potentially support the notion that adopting early reproduction and fast life history norms may not be due to gaps in adolescents' knowledge or understanding of sexual risks, but rather that pro-natal norms develop in line with the type of behaviour that will most assist in their reproductive success. More research should be conducted to determine if adolescents with fast life history strategies not only have
developed stronger pro-natal norms but also have gaps in understanding of sexual risks, as this would have considerable policy implications.

More generally, adolescents who favoured future rewards over immediate rewards reported wanting fewer offspring. Discount preference was also marginally associated with adolescents' ideal reproductive timing. The link between fertility scheduling and future discounting is already well established (Daly & Wilson, 2005) and my findings offer additional support for the concept that there is a trade-off between reproductive effort now and parenting effort in the future (Gangestad & Simpson, 2000). Individuals who perceive the future as dangerous may take the immediate reward rather than wait for an uncertain return.

In the same way they may desire more children because not all may survive, or intend to reproduce now rather than later. Those for whom the future holds more perceived opportunity can afford to wait for a bigger monetary payoff and to invest more in fewer offspring who they are confident will survive and reproduce. There was a significant interaction between sex and discount preference, with the association stronger for males in my sample. This might represent different levels of investment in future offspring between males and females, due to sex differences in potential reproductive rates (Clutton-Brock & Parker, 1992). Such patterns of risk taking, and strategic tradeoffs, would fall in line with predictions put forward in the framework of life history theory.

### 6.2.4 Kin networks

Grandparental investment was marginally associated with adolescents' future reproductive intentions, with closer relationships with grandparents predicting later fertility intentions. In addition, there was a significant sex by grandparental investment interaction, with the level of grandparental investment a stronger predictor of the reproductive timing of female adolescents in my sample. This goes against the predictions that those distant from
grandparental and kin networks may perceive the cost of childrearing to be much greater and therefore choose to delay reproduction until they are in a secure financial position and able to afford child caring assistance from non-kin (Sear & Dickins, 2010). However, as has been discussed (see Taylor, 1992), there is also the potential that the close kin networks that may promote cooperative breeding efforts may instead lead to resource competition between kin that undermines any cooperative benefits. Close kin ties that span multiple generations may also signal a low mortality environment consistent with later age of first birth (Low, Hazel, Parker, & Welch, 2008). On the other hand, adolescents in my sample who reported more grandparental and parental investment want more children. There was also a significant sex by parental investment interaction, with a stronger effect of parental investment on increasing the desired number of offspring for male adolescents. This suggests that grandparents may potentially offer assistance in terms of childrearing support and expertise, which does lend support to the idea that close kin ties can embed adolescents in a cooperative breeding network. Whether or not close kin networks promote or hinder cooperative breeding is an area that needs more research to further my understanding of this complicated and multi-faceted association. There are two directions of study I propose to shed more light on the issues of kin support and reproductive intentions. The first is what role physical proximity plays in understanding the impact of grandparental investment. Research on a Dutch cohort found that maternal grandparents were more likely to maintain frequent contact with their grandchild as the geographical distance between them increased (Pollet, Nettle, & Nelissen, 2006). Further research should look into what effect physical proximity has on levels of parental investment to further understand the opposing theories regarding associations between competition, kin investment and any direct reproductive benefits. Not living in close proximity with kin would perhaps remove direct resource competition which would potentially increase the kin directed benefits from being embedded in a cooperative breeding network. Secondly, examining different types of grandparents together (maternal and paternal) may be masking the different influences each
can have on grandchild bearing and fitness. In general, evolutionary studies have documented differential levels of investment in grandchildren based on genetic relatedness and the sex of the grandchild (Fox et al., 2010).

### 6.2.5 Chronic and acute stress

One potential explanation for the main findings of this thesis is that it has been an exploration of how stress adjusts individuals’ life history strategies. While the underlying proximate mechanisms at work are not known, a plausible suggestion is that there is an activation of stress response systems, similar to the activation triggered by the cold-pressor test. However, the main body of research examining the association between stress and life history strategies in humans, including the work presented in Chapters 2 and 3 of this thesis, is correlational and focused on the ongoing stressors as opposed to acute, short-term stress (Belsky, Steinberg, & Draper, 1991; Bogaert, 2008; Nettle, Coall & Dickins, 2011; Quinlan, 2003). In Chapter 4, however, I go further and look at how acute stress may have the potential to cause similar behavioural shifts and how this may cause differences in behavioural variation for individuals with different stress response systems.

Research on behavioural decision making has noted that not only are many decisions made under stressful conditions but also that many decision situations elicit stress responses themselves. Thus, stress and decision making, and potentially stress and reproductive decision making, are closely connected. This connection lies not only on the behavioural level, but also on the neural level, as research has shown that the brain regions that underlie intact decision making are regions that are sensitive to stress-induced changes (Starcke in refs & Brande, 2012). For example, females must begin a suite of hormonal and growth changes by middle childhood to successfully reach menarche in preparation for childbearing at younger ages. Since cortisol is a major regulator of sexual development and fertility,
experiences of environmental stress may influence the reproductive axis at key switch points during development and puberty (see Ellis, 2004, for a review). Thus, encountering stressful environments and dealing with chronic stressors in childhood direct an individual towards strategies that are adaptive under ecological conditions (Ellis, Shirtcliff, Boyce, Deardorff, & Essex, 2011). However, causally exploring the effects of acute stress on life history strategies is less well understood.

Therefore, I conducted two cold-pressor experiments to examine the effect of acute stress on females' life history preferences. On the basis of previous experimental research (Mathews & Sear, 2008; Brody, 2002; Lancaster, Hazard, Colbert, & Sinervo, 2008), as well as observation of real world responses to both high stress events (Cohan & Cole, 2002; Rodgers, John, & Coleman, 2005), and prolonged environmental stressors (Davis & Werre, 2007; Ellison, 2001) my core prediction was that acute stress will accelerate female life history preferences. Furthermore, I predicted that there would be an interaction between that effect and the individual's previous exposure to chronic stressors during childhood development. In short, I predicted that individuals with higher reported levels of exposure to early childhood stress would have strong stress response patterns to acute stress causing them to report different ideals than individuals with lower levels of reported early childhood stress.

Our findings suggest that physiological stress may be sufficient to shift women's preferences towards early reproduction and that acute stress has potential to adjust aspects of an individual's life history strategies, specifically their reported ideals in terms of reproductive timing and age of marriage. Furthermore, as predicted, individuals’ different exposures to chronic stress and subsequent life history trajectory caused individuals to respond to the stress paradigm with different behavioural patterns. I showed that individuals who reported more exposure to more early childhood stress responded to the acute stress condition by
reporting wanting to get married and have children earlier than women exposed to less early childhood stress.

A question that remains open is how acute stress in the short term might translate to a fast life history strategy in the long term. A useful analogy might be the way a spring is extended by a force. Up to its elastic limit, a spring will return to its original length when the force is removed. But after that limit the spring will undergo plastic deformation and will remain somewhat extended after the force is removed. In the same way, perhaps women's life history preferences may be elastic until some limit of stress is reached, at which point they become plastic. Individual differences in where that limit is, and how they react after the limit, may be analogous to the different elastic limits and plastic deformation curves of different materials. Therefore, I believe it will be of interest and importance to extend this study, running further cold-pressor experiments and recruiting participants from a broad socioeconomic spectrum with different exposures to chronic stress and on different life history trajectories, to further explore the impact of acute stress on reproductive intentions and the interaction between acute and chronic stress on variation in reproductive timing.

6.3 Future directions

6.3.1 Investigating strategic behavioural variation

A key finding of this thesis was that individuals with different levels of exposure to chronic childhood stress and on different positions on the socioeconomic gradient seem to respond differently to environmental inputs. Individuals exposed to low levels of developmental stress become more conservative in response to environmental inputs such as the sex ratio and acute stress, as they invest in somatic rather than reproductive effort and wait for “the storm to pass”. By contrast, individuals exposed to higher levels of developmental stress respond
to immediate conditions with more risky patterns as they shift towards reproductive effort in case environmental mortality means they will die before producing enough offspring.

This response pattern is predicted by life history theory regarding how individuals adapt their behavioural responses to environmental conditions, and is supported by a previous study of animal behaviour. Lancaster et al. (2008) looked at reproductive behaviour in female side-blotched lizards who have evolved both slow and fast life history strategies. By administering corticosterone (a hormone released in response to stress) to the female lizards, they discovered that the slow strategists delayed reproduction, while fast strategists accelerated it. Likewise in humans, I demonstrated that individuals on different life history trajectories respond in similarly strategic ways to the presence of acute stress based on their previous exposure to chronic stress. Therefore it is vital to extend this study to test young women from a broad socioeconomic gradient with different histories of developmental stress to explore how they respond differently to acute stress. In addition this would serve to further the understanding of whether or not physiological stress is a key proximate mechanism that calibrates human behaviour and reproductive strategies.

If stress does affect life history preferences, as my thesis suggests, it might also affect mate preferences. This is because women who are pursuing different reproductive strategies prefer different kinds of men. When looking for short-term relationships, which are characteristic of a fast life history strategy, women prefer masculine men exhibiting characteristics associated with testosterone (Little, Jones, Penton-Voak, Burt, & Perrett, 2001). This is thought to be because testosterone is associated with heritable benefits but lower investment in offspring (Archer, 1980). This idea is supported by cross-cultural research showing an association between pathogen prevalence and women’s preferences for more masculine faces (Gangestad & Buss, 1993; DeBruine, Jones, Crawford, Welling, & Little, 2010). Experimental evidence is scant, although in one study physiological stress influenced men’s mate preference (Lass-Hennemann et al., 2010), although correlates of
testosterone were not investigated. Supporting evidence from animal research suggests that stress can alter animal mate preferences (Lopez, 1999; Kavaliers & Ossenkopp, 2001). Therefore another direction in which to extend this thesis would be to test whether stress increases women’s preference for masculine faces.

It would also be of interest to explore the link between acute stress and individuals’ judgements of emotional stimuli, as the ability to identify emotions is central to social functioning. The hypothalamic-pituitary-adrenal axis is activated by stress and also when responding to challenges involving social evaluation or a threat to social/affective relationships (Schwabe, Haddad, & Schachinger, 2008). Furthermore, men and women are expected to respond differently to stress, as women have a “tend and befriend” response to stress, whereas men decrease affiliative behaviour (Taylor, 2006). An unexplored possibility, therefore, is that stress alters the way men and women process emotional stimuli. If stress does alter people’s perceptions there are important implications for predicting how men and women will respond under stressful conditions. Upon seeing a facial expression briefly, a stressed man may perceive it as aggressive, possibly leading to violence or avoidance, whereas a stressed woman may perceive it as friendly, leading to affiliation.

6.3.2 Policy implications

In general the focus of policy in the UK directed towards reducing teenage pregnancy rates has been on simple proximate correlates of early fertility without understanding human behaviour as adaptive to environmental conditions. Such policy has often focused on the health concerns or moral issues surrounding early childbearing (as in the Social Exclusion Report in 1999). This approach is unlikely to be successful if adolescents continue to live in deprivation and perceive their environments as being hazardous, react to acute stress in patterns that fit with their life history profile, have experiences in their family and
neighbourhood that truncate their future expectations and, in consequence, make a reproductive decision to begin to conceive children at a young age.

Firstly, a new approach is needed; one that seeks to understand early fertility and to develop interventions based on the principles of life history theory and that sees humans as inherently local creatures, responding to cues in their immediate environment about the availability of mates and chances of living a long, predictable life. Politicians point towards inequality and deprivation and these environmental conditions are the reality, yet policy makers should not expect individuals to make choices that conform to wider societal norms if these choices are not rational for the individual who must consider the risk and resources of their immediate environment. What is, therefore, required next is a theoretically guided approach to understanding behavioural decisions made by particular individuals in particular neighbourhoods. This will require a focus on perceptions of risk, social network structures in terms of kinship and other support groups, availability of mates and local competition and individual responses to acute stress. In short, a different kind of data resource is required to inform policy (Nettle, 2011).

Furthermore, the findings of this thesis suggest that politicians and those working in the media should no longer view teenage parenthood as a problem of limited education or irrational risk taking, but rather the result of strategic decisions made within certain environmental conditions. For example, policy makers should consider early childbearing within a broader suite of fast life history traits where traits such as not being so interested in education, seeking short term satisfaction, not saving enough money for the future are all adaptive in conditions of environmental harshness and uncertainty. All of which, including early childbearing, feed into large societal issues. Policies aimed at reducing teenage pregnancies or supporting teenage mothers should, therefore, not focus on a lack of sexual knowledge or random reproductive accidents. A further benefit of this new view would be to remove the stigma often associated with young parenthood. This would also help remove
the counter-intuitive notion that teenage pregnancy prevention policies will act to reduce poverty and social exclusion and would acknowledge that the situations women are living in contribute to the timing of reproduction (Geronimus, 1991, 1992). Policy approaches would ideally aim at providing deprived women and girls with the chance to live long, healthy, predictable lives (Geronimus 1996). Attempts should be made to reduce all types of inequality including personal perceptions of inequity, and interventions should be aimed at individuals” perceptions of relative poverty and extrinsic mortality risks, and responses to these stressful living conditions perhaps through developing a targeted cognitive behavioural therapy, all of which should eventually affect and shift reproductive behaviour.

6.4 Conclusions

The objective of this thesis has always been to move towards an integrated understanding of human reproductive and behavioural variation. This thesis has looked both at the ecological questions about ultimate causes (i.e. how is variation in reproductive timing adaptive to environmental conditions), and the psychological questions about mechanisms that influence behavioural adaptations (i.e. what is the role of intrasexual competition, subjective perspectives of environmental quality, etc.).

Through adopting a behavioural ecological stance in considering human reproductive variation this thesis has highlighted the central importance of understanding human behaviour as adaptive to local environmental conditions. In addition my research suggests individuals’ perceptions of environmental risk and extrinsic risk to their own mortality and acute stress responses play an important role in influencing fertility intentions. Together these findings highlight the importance of understanding life history trade-offs as central to reproductive scheduling.
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