Chapter 7

Parenting and families

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Introduction

Parenting in *Homo sapiens* is rather different to parenting in most other primates. Our long developmental period and relatively short birth intervals mean that offspring are 'stacked', with mothers having to simultaneously look after several dependent children at different developmental stages. This creates a high burden of care for mothers, which mothers appear to alleviate by co-opting other relatives into helping out. This cooperative breeding strategy introduces complexity into 'parental' investment: various individuals may be investing in children, not just parents, but also grandparents, older siblings of the child and potentially step-parents. The stacking of human offspring also introduces complexity into the allocation of parental investment across children within the same family, given that a number of children of different ages will be competing with one another for parental resources.

This chapter surveys the relevant literature on human parental investment. It first introduces parental investment theory, and then discusses the issue of who invests in human children. Mothers clearly invest, but who else helps out? This section ends with a brief discussion of familial conflict, since family relationships may be competitive, as well as cooperative. The second half of the chapter starts by considering what is invested in children, and then moves on to a detailed examination of who is invested in, with particular reference to parental investment biases according to sex and birth order. Throughout, ecological variation in parenting and parental investment patterns are considered.

What is parental investment?

Parental investment is defined as any action by a parent who benefits an offspring at some cost to the parent. The concept was originally formulated by Trivers, who defined parental investment rather precisely as investment in an offspring which results in some cost to the parent's ability to invest in other offspring (Trivers, 1972). Subsequently, Clutton-Brock (1991) broadened the definition to include investment in offspring which has a cost to *any* component of a parent's fitness, including mating success or somatic maintenance. Parental investment is a key concept in life history theory (LHT; see Lawson, in this volume). Given a limited energy budget, LHT predicts that parents have a number of decisions, or trade-offs, to make, in order to allocate energy appropriately to maximise their fitness (Roff, 1992; Stearns, 1992).

The three most fundamental trade-offs of LHT concern parental investment. First, any energy devoted towards parenting cannot also be used for other functions, such as mating or maintaining body condition. So parents must trade-off parenting effort with mating effort and with somatic maintenance. Second, since there is a trade-off between current and future reproduction, parents must decide how much to invest in a current offspring (or litter), in order to conserve energy for future reproductive bouts. Finally, parenting effort must be traded-off between quality and quantity of offspring. Parents may either produce many offspring but invest relatively little in each one (the quantity strategy), or produce few offspring but invest considerably in each (the quality strategy). Parents engaged in the quality strategy must then decide how to allocate investment between their offspring, since equal investment in each may not be the optimal strategy.

Our own species is one in which parents adopt the quality strategy, by investing substantially in a relatively small number of offspring. Human children are relatively altricial at birth (that is, relatively helpless, in contrast to many species which have precocial young, who are relatively independent of parental care from birth), and have an unusually extended period of childhood during which they are reliant on carers for provisioning and protection (Bogin, 1997). Children are not able to fully provision themselves until well into their teens or later: delayed maturity means they do not reach full adult size or strength into this age and our ecological niche, which relies on difficult to acquire foodstuffs, means that children must engage in a long period of learning before becoming proficient producers of calories (Kaplan et al., 2000; Hill, 1993). Even after maturity, the social and group-living nature of our species results in lifelong bonds between parents and offspring, so that parents may continue to invest in offspring by transferring resources, providing grandparenting services, and social support well beyond reproductive maturity. Before discussing in more detail exactly what is invested in children, and how this investment is shared out between children within the same family, we will start with a consideration of who invests in children.

Who invests in offspring?

Parental investment may come from mothers, fathers or both, but maternal investment is rather more common than paternal (Clutton-Brock, 1991). Explanations for this biased investment pattern have tended in the past to hinge on anisogamy (the difference in size between male and female gametes): it seems to make intuitive sense that females should invest more heavily than males throughout the period of parental investment, since the larger size of eggs compared to sperm means that females are committed to investing relatively heavily at the outset (Trivers, 1972). Recently, Kokko and Jennions (2008) have cautioned that such arguments, while superficially appealing, have logical flaws and that the full explanation for sex differences in parental investment may be relatively complex. The anisogamy argument for female-biased parental investment makes the Concorde fallacy, for example (Dawkins & Carlisle 1976). Decisions about whether to continue investing in an offspring should depend only on the future costs and benefits of investing or ceasing to invest in that offspring, and should disregard how much has already been invested (a strategy not adopted by the French and British governments, who continued to invest in Concorde long after it become obvious the aircraft was a poor economic bet because they did not want to be seen to have wasted the considerable amounts they had already invested).

Anisogamy, and the relative cheapness of sperm to produce, also provides a superficially appealing explanation for why males would do better to invest effort in attracting additional mates rather than investing in parenting – since each additional female fertilised may result in a greater increase in reproductive success compared to any incremental benefit obtained through improving the survival and reproductive prospects of existing offspring. But again, this argument needs some refinement. Although such a strategy of pursuing mates rather than investing in offspring may benefit males who are particularly successful at acquiring mates, every offspring has one mother and one father so that the average male will not succeed in fertilising large numbers of females. It is also not necessarily clear that investing effort in finding additional matings always increases reproductive success more than investing in parental care.

Kokko and Jennions (2008) suggest that a more cautious and subtle approach is taken to understanding why maternal care tends to be more common than paternal, taking into account a number of factors. These include: the importance of sexual selection, which will determine whether some males can lucratively adopt a mating-focused strategy; both adult and operational sex ratios (the former refers to the ratio of adult males to females, the latter to the ratio of sexually receptive males to females), which again affects the costs and benefits of searching for mates rather than caring for offspring; the effects of caring or competing on mortality rates, which will in turn affect sex ratios, and; the probability of paternity.

The considerable variation in this list of factors across species means that, though maternal care is numerically more common than paternal care, there are numerous species in which paternal care, either alone or alongside maternal care, is seen (Clutton-Brock, 1991). Male-only care is in fact the predominant mode of parental care in fish, though it is rare in other classes of animal and not seen in mammals. Biparental care is by far the most common mode of care in birds, seen in 90% of species (note, however, that biparental care does not necessarily mean that males and females contribute equally to parental care, just that both contribute; Cockburn, 2006). Female-only care is the most common mammalian pattern, where any kind of male care is relatively rare: direct care from males is seen in less than 5% of species and 9-10% of genera. Primate fathers seem to be at the caring end of the mammalian spectrum. Though female-only care is still seen in the majority of species, direct male care has been observed in 40% of primate genera (Kleiman & Malcolm, 1981).

One problem with quantifying paternal investment is that what fathers do for offspring can be difficult to identify. The statistics above refer to direct forms of parental care. This includes care directed towards an offspring which has an immediate effect on the survival or well-being of the young, such as feeding, carrying, or grooming. Indirect care is care performed in the absence of the offspring but which may also have an effect on its health or survival, such as territorial defence. The problem with counting indirect care as paternal investment is that its primary purpose may not be parental investment. Territorial defence will also prevent other males from gaining access to females residing within the territory, so that it may be mating effort which fortuitously happens also to improve offspring reproductive success. In fact, this problem applies more generally to male care, even direct forms of care: is male care always parental investment, or is it mating effort? If females prefer males who provide useful services to their offspring, then males may use caring for offspring to attract females, rather than solely for the purposes of improving the reproductive prospects of their offspring (Smuts & Gubernick, 1992).

A final complication with identifying paternal investment is that it can be difficult to determine whether the objects of male care are in fact his offspring, which is why the literature on this topic often refers to ‘male care’ rather than ‘paternal investment’. Maternal care, at least in species with internal fertilisation, such as birds and mammals, is more difficult to mistake. The biparental care which characterises most bird species was initially thought to be a clear-cut case of paternal investment, but the advent of DNA fingerprinting demonstrated that a surprisingly high proportion of chicks in the nests of some species were the results of extra-pair copulations and were not the offspring of the male caring for them (Petrie & Kempenaers, 1998). Male care which is consistently directed towards unrelated offspring may well be a form of mating effort, though it is also possible that it results from misdirected parental effort.

This brief zoological summary of who cares for offspring suggests that the subject is complicated. Observations suggest that where post-natal investment occurs it is most common from mothers alone, sometimes from both mothers and fathers and sometimes just fathers, but that the reasons for this variation are numerous and not yet fully understood. The next section covers the question of who cares for children in our own species.

Who invests in human children?

Clearly, mothers invest substantially. As with all mammals, human females are committed to gestation and a lengthy period of lactation, which typically lasts at least two years, often longer, in traditional societies (those without access to modern medical care or contraception, where both fertility and mortality tend to be high). A review of child mortality in such societies suggested that children who lose their mothers in the first year or two of life have very much higher risks of dying than those whose mothers are still alive, demonstrating the almost exclusive reliance of infants on maternal care (Sear & Mace, 2008; see Figure 7.1). The reliance of children on maternal care once they are weaned appears to be surprisingly low, however: the survival of slightly older children (more than two years) who lose their mothers is often remarkably high. Two-year-old children are clearly not able to feed and care for themselves, so some other individual(s) must be stepping in to invest in these children. The father of the child might appear to be the obvious candidate for this alternative carer, but is that what the evidence shows?

Insert Figure 7.1 about here

How extensive is paternal investment in humans?

Much of the evolutionary psychological literature gives the impression that paternal investment is universal and substantial in *Homo sapiens*. It is not uncommon for evolutionary psychologists to base arguments about our evolved mental architecture around assumptions that men invest heavily in children, and that women universally seek men who are willing and able to invest in children (Geary, 2000; Geary et al., 2004; Buss, 1989). These assumptions build on a long-standing belief amongst students of human origins that the provisioning of women and children by men has been of vital importance in human evolution, and led to many distinctly human characteristics.

This idea perhaps reached its apotheosis in a 1981 *Science* article by Owen Lovejoy on how the “origin of man” (sic) depended on behavioural shifts towards the nuclear family and extensive male provisioning of women and children (Lovejoy, 1981). This view has proved remarkably hard to shift (see e.g. Lawrence & Nohria, 2002) despite a concerted assault on this hypothesis over the last few decades by researchers attempting, and failing, to find evidence that heavy paternal investment is universal in our species. The alternative perspective, now accepted by much of the behavioural ecology community, is that the role of human fathers is very variable, and may be surprisingly inconsequential. Surprisingly, because children need substantial investment in order to reach adulthood as healthy, competitive adults (Hrdy, 2009).

Whether you consider human fathers to be paragons of paternal investment or somewhat paternally delinquent depends to some extent on your frame of reference. Geary (2000), for example, argues that compared to the average mammal, human fathers do seem to be unusually closely involved in their offspring: many men do maintain relationships and invest substantially in their offspring throughout childhood and beyond, in contrast to the majority of mammalian fathers who have no contact with offspring after conception. On the other hand, Hrdy (2008) points out that human paternal investment appears somewhat less impressive when only primates are considered, since primate fathers are rather more likely than the average mammal to engage in care of offspring. In some species, such as siamang (a South East Asian ape), titi monkeys, owl monkeys, and some callitrichids (marmosets and tamarins), male care is intensive and essential for offspring survival. For example, the father is often responsible for carrying infants, which incurs substantial energetic costs.

Yet in our own species, at least some fathers invest little or nothing at all. In post-industrial societies, a high proportion of divorced and never-married fathers lose contact with their children and invest little or nothing after the dissolution of the parental relationship (Seltzer, 1991). Hrdy (2008) even quotes a study which found that Americans are 16 times more likely to pay used car loans than their child support payments. A similar picture of variable paternal investment is found in traditional societies: the same review of child mortality which found much higher mortality for young children without mothers found that when the effects of fathers on child mortality are investigated, in only one third of studies (7 of 22) did the absence of fathers result in higher child mortality (Sear & Mace, 2008; see Figure 7.1). These results are not expected if fathers are always vital to the provisioning and care of women and children.

Despite their different perspectives, however, both Hrdy and Geary agree on the fact that paternal investment, unlike maternal investment, is facultative in our species: some fathers invest in their offspring and some do not, though they might disagree on the extent to which fathers invest. Given that there is agreement that paternal investment can vary both between both between and within populations, the next question becomes: what determines the extent to which a particular father will invest? A pre-condition of paternal investment is a social system in which fathers and offspring maintain bonds and can recognise one another (Chapais, 2008). Human societies fit this condition: in most, women and men form reasonably long-term unions, and even in the absence of such long-term bonds, men’s role in generating children is often understood so that biological paternity can be recognised (see Box 7.1 for a brief overview of the form of the human family). Given a set-up in which paternal investment is at least possible, how much individual fathers then choose to invest will be determined by some combination of the following factors: paternity certainty, and the costs and benefits of investing in offspring versus investing in additional mating effort (Kleiman & Malcolm, 1981; Kempenaers & Sheldon, 1997).

Insert Box 7.1 about here

What affects paternal investment: Paternity certainty

Paternity certainty refers to the probability that a man’s putative children (often operationalised as his wife’s children) are his own genetic offspring. Cross-cultural studies suggest paternity certainty rates are rather high in most human populations, but are not 100%. There is something of an urban myth that paternity uncertainty is widespread in humans, based on an unpublished study using blood group data which apparently estimated that 20-30% of children in one Liverpool towerblock were not the offspring of their putative fathers (sometimes known as the ‘Liverpool flats’ study, cited in Cohen, 1977). While paternity uncertainty might be this high under a particular set of circumstances, most human fathers appear to have a considerably higher confidence of paternity.

Anderson recently reviewed the cross-cultural evidence and suggested the range of paternity uncertainty was 1.9-3.9% (Anderson, 2006). Such low figures suggest either that women rarely conceive children through extra-pair matings, and/or that men are good at detecting any such children so that paternity is generally not mistaken. Low paternity uncertainty, therefore, does not necessarily imply the existence of lifelong and faithful pair-bonds. It simply means that, on the whole, paternity of children is usually correctly attributed. In ‘partible paternity’ societies, for example, such as some forager communities in South America, women form relationships with several men, often simultaneously (Beckerman et al., 2002; Hill & Hurtado, 1996). Children have multiple ‘fathers’ in these societies, since a ‘father’ is defined as any man who had sex with the mother during or around the time of pregnancy. But there is a hierarchy of such fathers, with ‘primary’ fathers being more likely to be the biological father, than ‘secondary’ fathers.

The study by Anderson (2006) did not include any partible paternity studies, and has been criticised for relying heavily on agricultural and industrialised societies (Hrdy, 2009), and including too few forager societies – as unfortunately do the majority of such cross-cultural studies given that relatively few foraging communities exist today. The advent of agriculture allowed the accumulation of wealth to a much greater extent than is possible in forager societies, which is likely to have changed relationships between men and women (Kaplan & Lancaster, 2003). When resources can feasibly be acquired and accumulated men tend to do so, in order to attract mates (Holden & Mace, 2003). In situations where men control resources, women become more dependent on men, and men's bargaining power within relationships increases. This allows them to demand exclusive sexual access to their wives, resulting in relatively high rates of paternity confidence. Whether men demand exclusive sexual access primarily because they do not want the paternal investment they intend to bestow on their children to be wasted on another man's child, or because they want to monopolise their wives' reproductive capacity and exclude other males from the mating pool is a question which is difficult to answer, given that both benefits are likely to accrue from mate-guarding.

Regardless of the exact level of paternity uncertainty, there is clearly at least some room for doubt in a man's relationship with his putative offspring. If he is considering whether to invest substantial resources in an offspring, he should take the risk of paternity uncertainty into account.

What affects paternal investment: Costs and benefits of parenting versus mating

The costs and benefits of investing in further mating effort rather than parenting effort will depend on both the availability of other mating opportunities, and on the sensitivity of offspring to male care. In our own species, whether children are heavily dependent on paternal investment for their health and well-being is often not empirically tested; instead it is simply assumed to be the case. It is worthwhile, therefore, to consider the evidence available on what it is that men do for their children, and what impact this has on the children. The forager literature has tended to focus on male provisioning of children, since this has long been assumed to be the father's main role in the human family. Cross-cultural analysis suggests that men do contribute substantially to production in hunger-gatherer societies, but so do women. On average, men bring back just over half the calories consumed by a group, women just under half (Marlowe, 2005). Similar results have been obtained when cross-cultural analysis is broadened to other subsistence strategies (Hewlett, 2000).

Some anthropologists working on African hunter-gatherers have questioned, however, whether the main purpose of the hunting that men do in such societies is the provisioning of children (Hawkes, 2004; Hawkes & Bird, 2002). Meat, particularly large game, tends to be shared fairly widely among the whole camp, rather than directed at the hunter's own children.

The ‘show-off’ hypothesis for hunting, then, suggests that men’s hunting efforts are at least partially directed towards attracting additional mates, rather than solely providing for children (Hawkes, 1991). The higher mating success of successful hunters attests to the success of this strategy (Kaplan & Hill, 1985).

Anthropologists working on South American foragers, in contrast, present evidence that most hunted game does end up with the hunter’s own family, and argue more strongly for hunting as parental effort (Gurven & Hill, 2009). This group has recently tried to devise tests which tease apart mating from parenting effort in the Tsimane (Bolivian forager-farmers) by investigating the patterning of direct male care, and concluded that their evidence shows more support for parenting rather than mating effort (Winking et al., 2009). Such research only highlights the difficulty of distinguishing the mating and parenting hypotheses, however, since the services men provide to children could serve both purposes simultaneously. Perhaps the only conclusion to be drawn is that hunting and other male efforts may serve as both mating and parenting effort, though the relative balance between the two may differ between societies.

There is similar confusion in the literature on non-forager populations about what constitutes paternal investment. In stratified societies, well-known links between higher paternal socioeconomic status or education and positive child outcomes have been cited as evidence for paternal investment (Geary, 2000). In the post-industrial world, fathers are of great interest to policy-makers, where they are assumed to be vital to a child’s functioning and success in this particular environment. A large body of research has suggested that children without fathers have poorer outcomes than those who grow up in intact nuclear families (see Sigle-Rushton & McLanahan, 2004 for a review). However, such patterns do not necessarily provide clear-cut evidence of paternal investment.

As stated earlier, in non-forager societies, most resources tend to be owned by males. Such societies involve the exploitation of subsistence niches which allow the accumulation of resources (including land in agricultural populations, animals in pastoralist communities, and money and other assets in market-economies), which men take control of in order to attract mates. These resources are then used to provide for children, but whether this is primarily mating or parenting effort is open to question. The positive relationship between paternal resources and beneficial child outcomes may be a side effect of male monopolisation of resources resulting in female preferences for male resources: in other words, men may accumulate resources in order to attract women; women then use these resources to raise children successfully. Disentangling mating from parenting effort may again be impossible, given that other forms of resource transfer can serve both mating and parenting purposes simultaneously, just as does the transfer of meat.

But fathers are not simply providers of resources, they can perform other services for children, such as protecting them from other males, direct care, teaching subsistence skills, and support in social interactions or conflicts. All these activities are likely to be beneficial for children (though this is rarely quantified), but again it is difficult to determine whether such behaviours can entirely be considered paternal investment, or whether mating effort might also be involved. The existence and extent of such behaviours certainly varies between societies, suggesting that they may be at least partially dependent on whether there are alternative mating opportunities available. The few tests which have attempted to determine whether this is a factor in paternal behaviour suggest that the relative ease with which men can find other mates is indeed important. Blurton Jones and colleagues (2000) investigated divorce in four forager populations, and concluded that the availability of alternative mating partners was a better predictor of divorce than the benefits that children gained from the presence of fathers. Again we return to the conclusion that paternal investment is facultative. What fathers do for children may well benefit them (intentionally or not), but there are at least some occasions when men will cut short such benefits if alternative reproductive options are available.

Proximate mechanisms of paternal care

One final piece of evidence on paternal investment relates to the proximate determinants of male care. Hormonal changes during and after pregnancy may promote maternal care in women (Ellison & Gray, 2009). Recent research suggests men also undergo hormonal changes in relation to their marital and paternal status, which may promote shifts in strategy between mating and parenting effort. In some populations, including our own, testosterone is lower in married than single men, and lower in fathers compared to non-fathers (Burnham et al., 2003; Gray et al., 2004; Gray et al., 2006). This may be correlated with the relative amounts of effort devoted towards attracting a mate compared to investing in children – the former may require competitive behaviour facilitated by high levels of testosterone, the latter more affiliative behaviours which require lower levels of this hormone.

Research emerging from non-Western populations, suggests there may be some variation in these hormonal shifts between populations. In a polygynous Kenyan sample, for example, testosterone was not lower in married compared to single men, possibly because in polygynous societies even married men continue to invest relatively heavily in mating effort (Gray, 2003). A Tanzanian study compared a high paternal care population, Hadza hunter-gatherers, with a low paternal care population, Datoga pastoralists, and confirmed the authors' prediction that testosterone would be lower in fathers in the high paternal care group, but not the low paternal care group (Muller et al., 2009). Such proximate, hormonal correlates of paternal status and paternal care suggest that men do have adaptations which allow them to shift into a parenting mode (or at least allocate a certain proportion of resources to parenting, rather than mating, effort) but that these adaptations are flexible and sensitive to environmental conditions.

In summary, paternal investment is facultative in our species. There is both inter- and intra-population variation in how much men invest in children, and exactly what they do for children. Male (not necessarily paternal) care and provisioning does seem important, however, given that the male contribution to the diet is often substantial. Whether this is primarily mating or parenting effort may be difficult to assess: it probably serves both functions. Rather than assuming that any act on the part of a male which improves child outcomes is paternal investment, it may be better to consider carefully exactly what men are doing and why.

Who else invests?

So fathers are contributing to child well-being, but these contributions vary quite substantially between and within populations, and are sometimes negligible. Does this mean that women who can rely on relatively little paternal support must absorb the full burden of raising children? It appears not, since raising human children is a very energetically intensive exercise, probably too expensive for mothers to manage alone. Women instead rely on help from other quarters. The question of whether humans are cooperative breeders has been raised in recent years, given this very heavy burden of parenting (Hrdy, 2005, 2009). Cooperative breeders are those species where non-parental care of young is common. Cooperative breeding is a relatively rare strategy, commonest in birds, where it is estimated that 9% of species breed cooperatively (Clutton-Brock, 1991; Cockburn, 2006). The strategy is less common in mammals, but a handful of species, including some canids, meercats, naked mole rats and callitrichids do it.

Recent research suggests that humans can be added to that list (Foster & Ratnieks, 2005). In our species it seems that relatives, particularly older women and pre-reproductive children, are the ‘helpers-at-the-nest’ who allow women to raise many dependent children simultaneously. It has been known for some time that children contribute considerably to the household economy, thereby effectively underwriting their parents’ subsequent fertility (Lee & Kramer, 2002; Kramer, 2005). Older individuals also may continue to be productive long after they have any dependent children of their own, suggesting grandparental, particularly grandmaternal, effort is important in our species (Bock & Johnson, 2008; Hawkes et al., 1989).

Grandmothers and older children are ideal ‘helpers-at-the-nest’ since they are not occupied with children of their own. Pre- and post-reproductive individuals do not, in fact, have the option of producing their own offspring. A hypothesis gaining ground is that the unusual feature of human menopause may have evolved precisely because of such beneficial grandmaternal effects (Hawkes et al., 1997; Shanley et al., 2007). It is certainly becoming clear that grandmothers are often very important to child well-being. Several evolutionary anthropologists have now tested the hypothesis that children with grandmothers present will have better outcomes, including survival rates, than those without grandmothers. A review of this literature found that maternal grandmothers were particularly beneficial, their presence improving child survival in just under 70% of cases (Sear & Mace, 2008; see Figure 7.1). Paternal grandmothers were also often beneficial, though less commonly than maternal grandmothers, improving child survival in about half of the populations studied.

It is difficult to assess the contributions of older children within the household, since sibling relationships are characterised by competition as well as cooperation, but there was evidence that the presence of siblings old enough to act as helpers-at-the-nest was also frequently beneficial to children (Sear & Mace, 2008; see Figure 7.1). An additional strategy which women can use to help raise children is to seek investment from men other than the child's father. Polyandrous mating, found in partible paternity societies, may be one such strategy which women use to confuse issues of paternity, and convince other men to invest in their children (Hrdy, 2000). Children with more than one father in such populations have been found to have higher survival rates than those with only one father (Beckerman et al., 1998; Hill & Hurtado, 1996). This may be brought about by the provisioning of breeding couples by other adult males, which has just been demonstrated in one partible paternity society (Hill & Hurtado, 2009). Overall this review provides empirical evidence that humans are indeed cooperative breeders, but that we adopt a relatively flexible cooperative breeding strategy, with help coming from many different potential sources, varying both between and within societies. 'Parental' investment may not just come from parents, but several other individuals too.

Familial conflict

The preceding section should not give the impression that family relations are always entirely harmonious. Within the family there is also considerable conflict. Trivers (1974) was the first to develop the concept of parent-offspring conflict. Parents and offspring will disagree about the optimal amount of investment given to each offspring. Parents in iteroparous species like our own must allocate their effort carefully between all their offspring to maximise fitness. But each offspring wants parents to invest more in itself than its siblings, since each offspring can gain greater fitness from its own reproduction than from that of its siblings.

This conflict between parents and offspring over investment has been well studied in the context of pre-natal investment. Haig (1993, 1996a) has suggested that the desire of offspring to extract more investment than the mother wants to give leads to an arms race during pregnancy. The foetus develops adaptations which try and extract as many nutrients as possible from the mother; the mother develops adaptations to protect herself from the foetus's demands. The foetus is at an advantage in placental mammals, since it has direct access to the mother's bloodstream through the placenta. Haig proposes that obstetric problems such as gestational diabetes and pre-eclampsia in our own species may result directly from the foetus's attempts to manipulate maternal energy supplies through placental hormones, and the mother's attempts to resist the foetus's manipulations.

Such conflicts during pregnancy may be exacerbated by conflicts between, not just the mother and foetus, but between maternal and paternal genes within the foetus (Haig, 1996). During a pregnancy the mother may be trying to keep resources in reserve for future reproduction, but the father of the child may not be related to any of the mother's future children. Paternal genes within the foetus may, therefore, be interested in extracting more nutrients from the mother for the current offspring than maternal genes. Such conflict may be implicated not just in disorders of pregnancy, but also behavioural disorders of children. Prader-Willi syndrome, for example, may be a disorder accidentally resulting from this conflict between maternal and paternal genes, as it is associated with behaviours which reduce the mother's costs of childrearing (and therefore represents a 'win' for maternal genes: Haig & Wharton, 2003).

Siblings will also compete among themselves for parental resources. Sibling competition reaches its most extreme form in siblicidal bird species (see Lawson, in this volume). Such within-family homicide is relatively unusual in humans, but is sometimes seen where very valuable resources are at stake. Historical accounts of the relatively homicide-prone Vikings have been analysed to demonstrate that the probability of an individual killing a close relative depended on the value of the resources at stake: high rewards were necessary before the murder of a relative became likely (Dunbar et al., 1995). Usually, however, sibling competition takes a more subtle form, involving variations in how much investment children can acquire from parents, observed as apparent biases in parental investment (discussed below).

What is invested?

Who invests in human children is relatively complex, but so too is the question of what is invested. Parental investment can be both pre-natal (for mothers only) or post-natal (all other investors). Pre-natal care involves investing somatic resources in offspring – mothers sustain pregnancy by directly transferring reserves of energy to the foetus. Mothers continue to invest somatically after birth, during breastfeeding. Mothers and other individuals have important roles in provisioning children after birth with food, and protecting and cleaning them – all activities which take time and therefore involve opportunity costs. Human children also need considerable investment beyond simply ensuring they survive to reproductive maturity in order to ensure they become productive and competitive adults.

All human societies, whatever mode of subsistence they use, involve skills which need to be taught to children. Such training takes more time, and may also involve the transfer of extra-somatic resources (those stored outside the body). Parents may continue to invest after offspring reach reproductive maturity. In societies which accumulate extra-somatic resources, parents commonly transfer such resources directly to children in order to launch them onto the marriage market, including bridewealth and dowry payments (the former involve transfers from groom's to bride's family, the latter from bride to groom). The final transfer which occurs from parents to children occurs after death, when parents pass on any accumulated resources to their offspring. Such transfers are still likely to be costly to the parent and therefore fit the definition of parental investment, though they occur after death, since resources may be accumulated with the express purpose of donating to children, and not used during the parent's own lifetime.

It is worth noting that parental investment is often measured indirectly. Determining exactly how much energy parents are transferring to children, how much time they spend on them and what extra-somatic resources are being transferred is not always easy. Instead, parental investment is frequently measured by determining its end result, the effects on the child (Borgerhoff Mulder, 1998). The following is a by no means compete list of variables which have been used as indicators of parental investment: child survival rates, nutritional status, immunisation rates, attendance at medical clinics, length of birth intervals, educational attainment, age at marriage, and inheritance bequests. Measuring child outcomes rather than parental investment itself is problematic since such outcomes are likely to correlate with, but may not match exactly, parental investment itself.

An additional problem with measuring parental investment in our species is that not all forms of investment are equal, so that different parental investment patterns may be been seen if different measures of parental investment are examined. Social scientists have made a distinction between base and surplus resources (Downey, 2001). The former are those required for basic survival and adequate health; the latter those that enhance child well-being and social competitiveness over and above that which is necessary to ensure survival alone. All children need base resources, but parents can choose to allocate surplus resources differentially between children. Such a distinction may be of lesser value in the evolutionary literature, since a child that survives but is not sufficiently competitive to reproduce successfully is not particularly useful in terms of Darwinian fitness, but still may have some heuristic worth.

For example, a study in rural Ethiopia found that biases in parental investment became stronger for ‘surplus’ resources (education) under conditions of reduced environmental risk, but not for ‘base’ resources (breastfeeding and immunisation: Gibson & Lawson, 2009), suggesting that parents do allocate varying types of investment differently. Distinctions should also be made between shareable and non-shareable resources (Downey, 2001). Certain forms of parental investment, such as parental energy reserves or extra-somatic capital, are non-shareable – any unit of energy or wealth given to one child cannot be given to another. But other forms of investment, perhaps certain types of teaching or, in modern societies, the presence of a computer in the household, can more easily be shared between siblings. Again different patterns of parental investment may be seen for shareable and non-shareable resources.

Who is invested in?

Perhaps the most commonly asked question in the parental investment literature focuses on who parents invest in. Parents do not necessarily invest equally in all their offspring, but will bias their investment towards those offspring likely to provide the greatest fitness return. As Hrdy (2000b) has pointed out, ‘mother love’, and therefore investment, is not automatic and unconditional, but will be contingent on the characteristics of both child and mother, just as paternal investment is facultative (the same applies to any other relative who may potentially invest in a child). Humans are relatively unusual among primates in that they will sometimes retrench entirely on post-natal parental investment, by abandoning or killing children (Daly & Wilson, 1984). This practice is likely to be related to the intense investment needed in human children after birth to raise them successfully to adulthood. While both infanticide and abandonment are relatively rare, they are known to occur at least occasionally in the majority of human cultures, and to occur in situations where the prospects of raising that particular child successfully are low. More common are more subtle manipulations of parental investment: all children might be invested in, but some are more invested in than others. This bias in parental investment has been investigated most intensively for two characteristics of the child: birth order and sex.

Birth order

At the simplest level, birth order is likely to affect the amount of parental investment children receive because of the trade-off between the quantity and quality of offspring, known in the social sciences as the ‘resource dilution’ effect (Downey, 2001): higher birth order children (that is, children with many older siblings) will receive less investment than lower birth order children since the former only exist in large families, and parental resources are spread more thinly in large, compared to small, families. In fact, all else being equal, the parental investment that each child receives will take the form of $y = 1/x$, where x is the number of children in the family. But all else is not equal. Children of different birth orders will differ systematically in other ways, so that much ink has been spilt trying to determine whether birth order in and of itself affects parental investment.

Both the social science and evolutionary literature is filled with studies investigating the effects of birth order on traits from personality (Sulloway, 1996), intelligence (Kristensen & Bjerkedal, 2007), and educational achievement (Travis & Kohli, 1995; Bock, 2002), to status (Davis, 1997) and career achievement (Lindert, 1977), to mortality (Manda, 1999; Lynch & Greenhouse, 1994) and anthropometric status (Lawson & Mace, 2008; Floyd, 2005), to sexual orientation (Bogaert, 2006), familial sentiment (Salmon & Daly, 1998), all the way up to reproductive success (Mace, 1996; Draper & Hames, 2000; Borgerhoff Mulder, 1998). The problem with this literature is that many studies fail to adequately control for the many factors which could cause spurious correlations between birth order and these outcomes, such as family size, socioeconomic status and parental resources, and the differing ages and needs of children (see Box 7.2).

Insert Box 7.2 about here

This has led to something of a backlash against birth order studies in the social science literature, and calls for much greater methodological rigour (Steelman et al., 2002; Wichman et al., 2006; Somit et al., 1996). Birth order research tends to be accepted somewhat less critically in the evolutionary literature, perhaps because there are good evolutionary reasons why parents should invest differently in children of different birth orders, regardless of resource dilution effects: children of different birth orders will differ in both age and the level and type of investment they require (which does not mean, of course, that such studies should not also be carefully assessed for methodological rigour).

Child’s age will affect predicted investment patterns because age is correlated with reproductive value. Reproductive value is defined as the expected future reproductive output of an individual, at a given age (Fisher, 1930). It is the product of both surviving and successfully reproducing, both of which vary strongly by age. In our species, mortality is highest immediately after birth, declines to a low point in late childhood, then begins a more-or-less continuous rise at adolescence before increasing rapidly among elderly adults (Gurven &

Kaplan, 2006). Reproductive value follows a similar path: newborn children have a relatively low reproductive value; it increases as children age before peaking at the average age at first birth, when individuals have a high expectation of future reproductive output (see Figure 7.2; reproductive value curves may also differ for sons and daughters).

Insert Figure 7.2 about here

All else being equal, then, older children have higher reproductive value than younger children, so that older children might be expected to be favoured over younger. This leads to the prediction that older children will always receive higher parental investment than younger, at least up to the point of sexual maturity. This may explain why early born children do frequently seem to be advantaged in a variety of outcomes. When infanticide occurs, for example, it is very commonly the younger child in which investment is terminated, not older children. Among Ache hunter-gatherers in Paraguay, a group in which rather remarkably high rates of child homicide are seen, 5% of all children born were killed in their first year of life, compared to about 2% of children killed per year between the ages of 5 and 9 (Hill & Hurtado, 1996). This conforms with findings from a cross-cultural survey that younger children, as well as those of low reproductive value for reasons of deformity or ill-health, were much more vulnerable to infanticide (Daly & Wilson, 1984).

Counteracting the trend for older children to get higher parental investment because of their greater reproductive value is that parents also invest according to the child's need or, more technically, the marginal value of that parental investment to each child (Clutton-Brock, 1991). A unit of parental care given to a ten-year old child may improve its survival chances slightly, but the same unit of parental care given to a newborn may increase the newborn's chances of survival much more dramatically. Newborns may, therefore, get more investment from mothers, in terms of both nutrition and time, because the marginal value of that investment is greater for younger children. Jeon (2008) has recently attempted to theoretically model the solutions to this dilemma for parents – should they invest more in older children because they have higher reproductive value or younger children because they derive greater marginal returns to investment? – and concluded that in the majority of cases parents should resolve this dilemma in favour of older children.

Perhaps the most extreme form of this favouring of oldest children is primogeniture: when the oldest child (usually in fact the eldest son) inherits all or most parental resources. While almost every pattern of bequeathing wealth from parents to offspring is seen in human societies – oldest son or daughter inherits (primogeniture), youngest son or daughter inherits (ultimogeniture), all children or all children of favoured sex inherit equally – primogeniture is the most common pattern, certainly where parents differentiate between children in their inheritance (Murdock, 1967; Hrdy & Judge, 1993). Such a pattern may stem from a couple of other advantages of investing in first-borns: firstly, that this gives parents more time to contribute to this child's reproductive success; and secondly, that investing heavily in the eldest child may well shorten generation times, which will ultimately increase the fitness of the parental lineage. Such extreme biases in parental investment are only seen where resource-holding is essential for reproductive success, however, and where resources are limited, so that bequeathing wealth to more than one child risks diluting that wealth until it becomes almost useless for reproductive success.

Patterns of investment by birth order may not always favour early-born offspring, or at least may not always result in a linear relationship between birth order and child outcomes. Firstborn children tend to have lower birthweights than later-borns (e.g. Magadi et al., 2001), though it is not clear whether this results from maternal investment decisions or confounding factors such as selection effects (women who are not particularly successful at reproducing will be over-represented among the mothers of first births). Hints that later born children do better than early born children in that they are able to produce more children than early-borns come from a study of southern African hunter-gatherers, the Ju/'hoansi (Draper & Hames, 2000: though this study did not control for potentially confounding factors). U-shaped effects of birth order have been found for the number of children produced, though not number of children reared to adulthood, for males in historical Finland (Faurie et al., 2009). Such patterns could partially result from the cooperative effects of elder siblings, and therefore children benefiting from non-parental investment. But Hertwig et al. (2002) have cautioned that unequal outcomes can arise from an 'equity heuristic', a decision rule stating that parents should invest equally in all their children. They argue that, even if at any one time parents invest equally across all offspring, middle-borns will always receive less cumulative investment than first- or last-borns because they never benefit from an exclusive period of parental investment (see Figure 7.3).

Insert Figure 7.3 about here

Thus, a 'middle-born disadvantage' can arise even if parents show no bias towards any of their offspring. This is based on the assumption, however, that parents only invest while children are resident in the parental household, which is likely not to hold across all measures of parental investment in our species, since parents continue to invest in children throughout their lives. One final complication is that, where parents invest unequally in sons and daughters (see next section), the equity heuristic will not hold. In this case, what may be relevant to the child is same-sex birth order, so a modification of the middle-born disadvantage might be that it will only hold when same sex siblings are considered, as in historical Finland where a middle-born disadvantage in fertility was seen only for male offspring (Faurie et al., 2009).

Sex-biases in investment

One of the richest veins of literature on parental investment is on sex biases in parental investment. In a population with an even sex ratio, the average number of grandoffspring produced by a son and a daughter will be the same but, given that the variance in reproductive success differs between the sexes (usually, but not always, higher in males), the riskiness of producing sons rather than daughters will differ, sons being the higher risk sex in populations where male variance in reproductive success is higher than female. More importantly, parental investment may have differential impacts on sons versus daughters. Under certain circumstances, a unit of parental investment may be more valuable to a son than a daughter, if it can increase his reproductive output relatively more than the same unit of parental investment given to his sister.

This is the principle behind what is perhaps the most common framework for investigating sex biases in investment: the Trivers-Willard hypothesis (TWH: Trivers & Willard, 1973). As formulated for non-human species, it concerns pre-natal investment and states that, if three conditions hold, then the sex ratio at birth (SRB) should vary in predictable ways. These conditions are: (1) that the condition of the mother (investor) is correlated with the condition of the young at the end of the period of parental investment; (2) that the condition of the young at the end of parental investment should endure into adulthood and; (3) that one sex should benefit more from good condition than the other.

Typically, males benefit more from good condition than females: given the generally greater variance in male than female reproductive success, males in good condition can out-compete poor condition males and achieve high reproductive success. Females in good condition may also out-compete females in poor condition, but the discrepancy between females in good and poor condition will be much less than the discrepancy between males in good and poor condition (see Figure 7.4). So the TWH predicts that mothers in good condition will produce relatively more sons and mothers in poor condition will produce relatively more daughters.

Insert Figure 7.4 about here

Numerous attempts have been made to find evidence of the TWH in SRBs in our species, with varying degrees of success (see Box 7.3 for the typical SRB of our species). Most of these have measured parental condition as ‘status’ (including wealth, education and social class): Lazarus (2002) reported that of 54 analyses in the literature testing the TWH in humans, 26 (48%) supported the hypothesis. Fewer studies have attempted to test the TWH using measures of physiological condition, but with similarly mixed results. A strong effect of lower nutritional status resulting in more female births was found in a poorly nourished Ethiopian population (Gibson & Mace, 2003; see Figure 7.5). Lower pre-pregnancy energy intake was also found to correlate with fewer male births in a British sample (Mathews et al., 2008), but Stein and colleagues (2004) found no effect of acute undernutrition on SRB during the Dutch famine. The British study rather unfortunately also reported that women who ate breakfast cereals were more likely to produce boys, a somewhat unlikely finding which was widely reported across the media and raised doubts in the minds of other scientists as to the quality of the study (Young et al., 2009). Such a finding, which could easily be interpreted as a statistical quirk, highlights one of the potential problems with finding a Trivers and Willard effect: any effect sizes are likely to be small, which makes identifying such biases in the SRB statistically challenging (Gelman & Weakliem,2009).

Insert Box 7.3 and Figure 7.5 about here

A wider problem with identifying the Trivers and Willard effect is that many studies do not demonstrate the three conditions necessary for the TWH to hold in their study populations (Brown, 2001), nor do they give much thought to the mechanism by which biased sex ratios could be brought about. Some authors do attempt to test the pre-conditions (e.g., Cameron & Dalerum, 2009), and some are attempting to tackle the latter problem (e.g., Grant, 1998) but, as with birth order studies, research investigating the TWH in human populations should be judged on its individual merits.

In addition to SRB studies, there is plentiful research investigating whether the TWH holds for post-natal investment. In some respects, patterns of biased post-natal investment should be easier to investigate, since the mechanisms of biased post-natal investment can potentially be investigated directly (Cronk, 2007). At least some such studies have also attempted to determine whether the pre-conditions for the TWH hold, in particular whether the reproductive success of sons and daughters differs by parental status. Even if manipulating sex ratios before birth is mechanistically tricky, infanticide may be used as a means of postnatally adjusting the sex ratios of children. Dickemann's (1979) classic study of historical literature in Asia and Europe observed that female infanticide was much more common among upper social strata: she cited one high caste Indian group which claimed never to have let a female child born within the caste to live. This fits with the TWH since high status males are more likely to find wives than low status males, given that hypergyny is common in stratified societies (women, but not men, can marry into higher social classes). High status females, on the other hand, will face fierce competition for mates in the few social strata where marriage is acceptable for them, whereas low status females should have no trouble finding marriage partners.

Biased parental investment does not need to be as extreme as infanticide, however. Patterns of parental investment favouring girls, but which stop short of infanticide, have been found in two contemporary populations. Mukogodo pastoralists in Kenya (Cronk, 1989) and Hungarian gypsies (Bereczkei and Dunbar, 1997) show preferential treatment of girls in terms of, variously, breastfeeding duration, medical treatment, and education. Both are societies in which females have higher potential reproductive success by marrying into neighbouring wealthier groups, whereas males face competition between men from both within and outside the community for mates. At a much later stage in development, Mace (1996) interpreted a bias in inheritance patterns towards males in Gabbra pastoralists in Kenya as adaptive within a society where males benefit much more from inherited wealth (by becoming polygynous) than females do. This particular parental bias cannot be ascribed to the TWH, since all parents give wealth to sons in this society, but fits in with the principle which can be generalised from the TWH that parents will invest their resources strategically in order to gain the greatest fitness return.

The TWH is not the only candidate for explaining sex-biased parental investment, just the most tested. Other possible explanations are local resource enhancement (Emlen et al., 1986) or local resource competition (Clark, 1978; Silk, 1983). In the former case, children who enhance their parent's reproductive success, for example, by helping out with childcare may be favoured. In the latter case, children that compete with parents or other siblings for local resources may be disfavoured. Biased breast-feeding patterns in favour of daughters have been suggested to result from local resource enhancement effects in two populations where daughters are known to provide childcare: Hutterites (a north American Anabaptist sect: Margulis et al., 1993, and a Caribbean community: Quinlan et al., 2005). As previously noted, daughters frequently provide childcare and other services to mothers, but daughter-biased investment tends to be relatively uncommon. Instead, such explanations will only apply if daughters are particularly helpful compared to sons, which appears to be the case at least in the Caribbean example: a matrifocal society which girls are more productive than boys within the household (Quinlan et al., 2005).

Local resource enhancement/competition explanations are sometimes explicitly given by parents as the reason why sons are favoured in patrilocal societies, where sons stay in the family home and contribute to the household economy, but daughters marry out ("daughters are like crows, you feed them then they fly away"). That more contemporary societies are patrilocal rather than matrilocal may explain why stated preferences tend to be much more common for male rather than female offspring (Arnold 1992), though we should perhaps interpret such statements with caution, since what people say and what they do are not necessarily the same thing. Pennington and Harpending (1993) documented what appeared to be daughter preference in the Herero, cattle pastoralists in Botswana: girls were much more likely to survive childhood than boys. The authors attributed these effects to local resource enhancement: daughters brought in cattle at marriage, which could be used to marry off sons. But the Herero themselves did not attribute the higher survival of girls to daughter preference (at least in conversations with anthropologists). Instead, they claimed this was the result of witchcraft directed at women with many sons, stemming from jealousy of such fortunate women. The authors' own observations, along with those of nearby ethnic groups, however, attributed this discrepancy squarely to biased parental investment, in particular noting that the Herero simply did not feed their sons as well as their daughters.

Interactions between birth order and sex biases

The complicated nature of both birth order effects and sex biases in parental investment means that neither should be examined in isolation. The combination of the differential costs of raising boys and girls, the differential reproductive returns of each, plus local resource competition and enhancement effects often mean that a simple preference for boys or girls, or children of a particular birth order are not seen. Even in societies with a clear expressed preference for sons, certain sons may be more favoured than others, just as some daughters may be less discriminated against than others. Discrimination against girls may be particularly harsh against girls with many older sisters, showing up as increased mortality rates for such girls (Das Gupta, 1987; Muhuri & Preston, 1991). Similarly boys with many older brothers may be discriminated against even in societies which apparently bias investment towards sons: in Gabbra pastoralists, later born boys receive relatively little inherited wealth and marry age at a later age than their elder brothers (Mace, 1996).

Borgerhoff Mulder (1998) investigated parental biases by both birth order and sex in an attempt to distinguish between the TWH and local resource enhancement/competition models in

Kipsigis agropastoralists in Kenya. She found that the results varied according to measure of parental investment. A TWH effect was evident in education, for example, with richer parents favouring sons and poorer parents favouring daughters, which was consistent with stronger effects of wealth on the reproductive success of males than of females in this population. There was also evidence of both local competition and enhancement between siblings, however. Brothers seemed to compete reproductively with one another, but gain benefits from sisters, so that parents invested more in sons with few brothers and in sons with many sisters. Girls were less affected by their siblings and predictably also experienced less biased parental investment according to their number of brothers or sisters. Borgerhoff Mulder's (1998) conclusion was that studies of parental investment biases should consider a broad range of socio-ecological factors constraining parental options and payoffs, the value of children and the costs of parental investment, as well as which measures of investment are appropriate for comparing investment patterns between the sexes and between classes, an appropriately holistic conclusion with which to leave the subject of parental biases between children.

How parental condition affects who is invested in

One further factor to consider when investigating parental investment is the characteristics of the parent. Just as the child's reproductive value varies with age, so does the parent's, more precisely, parental reproductive value will decline throughout the reproductive period. This may influence parental decisions on whether to invest in children. Abortion and infanticide rates are higher among young than older women, since older women have fewer opportunities to replace such children (Daly & Wilson, 1984; Lycett & Dunbar, 1999). It will also influence how much to invest. A well-known hypothesis, but one which has so far received relatively little support, is the terminal investment hypothesis (Williams, 1966). This states that parental investment should increase in later, and particularly last-born, offspring, since there will be no need to conserve resources for future children.

There is some support for this hypothesis in our species in that rates of twinning and children born with genetic abnormalities increase with maternal age (Forbes, 1997). This has been suggested to result from a relaxation of the screening process which screens out less than optimal conceptuses in younger women. Since such screening mechanisms may result in false positives, where healthy foetuses are terminated in error, a relaxation of such mechanisms may result in at least some chance of a healthy birth for older women (Forbes, 1997). Otherwise, the evidence for terminal investment in humans is not strong, perhaps because other aspects of parental condition may also change with parental age (Fessler et al., 2005).

Other parental characteristics which change with age, and which may result in higher investment towards the end of a parent's reproductive life are experience and accumulated resources. Increasing experience may explain why first births are at particular risk of dying (Hobcraft et al., 1985). In societies with inherited wealth, resources tend to accumulate with age, and in wage economies, salaries may increase with age and experience. Food production in subsistence societies may follow a more curvilinear pattern, with younger and older adults relatively less efficient than adults in middle-age, as it is often related to changes in physical condition and strength (Hill & Hurtado, 1996; Bock & Johnson, 2008). It is this decline in physiological condition with age which may prove the nail in the coffin of the terminal investment hypothesis. A recent theoretical investigation by McNamara et al. (2009) found that, if both changes in parental reproductive value and parental condition with age are factored into the model, then parental investment is predicted to decline, and not increase, with age, suggesting that constraints on behaviour need to be carefully considered as well as the behaviour's potential adaptive benefits.

The role of environmental quality and risk

To finish this section on parental investment, we should consider the effects of environmental quality and risk – both of which will affect parental condition, ability to invest and the potential payoffs to investment. Environmental risk may affect both overall parental effort and how biased parental effort is. High risk may result in reduced effort overall: if parents cannot predictably ameliorate environmental risks to their offspring, there may be little point wasting effort trying to do so (Quinlan, 2007). High environmental risk may also result in a 'bet-hedging' strategy whereby parents discriminate little between children in investment, since they are unable to determine with confidence which children will survive and prosper. Such a strategy has been observed among educational investment in South African children (Liddell et al., 2003).

Similarly, chronic conditions of resource scarcity may result in relatively low investment and limited discrimination between children, since under such conditions parents are unable to fully control their children's survival and reproductive chances. As resources become more abundant, parents become more biased in their investment, as heavy investment in few children becomes a safer bet. Evidence for this can again be seen in educational investment in two African populations, in rural Ethiopia and Malawi. In both societies, birth order biases in educational outcomes are stronger in wealthy, compared to poor families (Gibson & Sear, 2009). This increase in biased parental investment, and shift towards investing heavily in few, rather than little in many, offspring, has been proposed as an explanation for the fertility decline which is now universal across human societies (Mace, 2007).

Conclusion

The human species is one characterized by intensive parental investment, but also one where ‘parental’ investment may come from individuals other than the child’s parents. The evolution of the human family, as well as some of our physiological traits, may in fact have been guided by the need for parents to involve other relatives in the raising of expensive children, at different developmental stages. Our long period of dependence, requiring a transfer of skills as well as resources, introduces further complexity into ‘parental’ investment: what is invested also takes many different forms, both somatic and extra-somatic, and different patterns of investment may be seen for different types of investment. Measuring parental investment therefore requires a careful consideration of who invests, what is invested, who is being invested in, and in what kind of environment is the investment taking place, as well as carefully controlling for the many potentially confounding factors which could influence the measurement of such investment.

The existing literature does not always take such a careful approach to the analysis of parental investment, so that it is important to carefully assess each study on its own merits. Such problems of measurement and methodology particularly beset the literature on birth order and sex-biases in parental investment, but are not absent from any section of the literature. Current research is rightly beginning to focus on getting the methods right in order to properly understand parental investment strategies (e.g. using advanced statistical techniques to control for confounding factors when investigating parental biases in investment: Lawson & Mace, 2008), and also beginning to test between alternative hypotheses for parental behaviour (essential if progress is to be made in interpreting parenting patterns: e.g. Winking et al., 2009).

This chapter has taken a broad-brush approach to evolutionary psychology: much of the research described in this chapter has been done by evolutionary anthropologists and behavioural ecologists, who have been traditionally more interested in questions surrounding family relationships and parental investment than evolutionary psychology in the most narrow sense, whose focus tends to be on sexual selection. The emphasis of the former disciplines on traditional, high fertility societies has led to a growing understanding of parental investment in small-scale, subsistence economies, but a dearth of evidence of parenting strategies in industrialised, low fertility societies. These disciplines also tend to ignore the mechanisms by which particular behaviours are brought about. In order to fully understand parental investment strategies, evidence needs to be gathered from a range of environments in order to assess commonalities and variation in parenting, and an obvious way to fill the gap would be to expand parental investment research in modern societies (an exception is perhaps grandparental investment, which is not entirely neglected in industrialised societies: see, for example, Coall et al., 2009 and Euler & Weitzel, 1996). Social scientists have collated a large body of research on parenting in modern societies, but since they do not work within an evolutionary framework they do not always ask the questions that have relevance to evolutionary debates about parental investment. More evidence could also be gathered on the proximate determinants of parental care and the mechanisms by which biases in investment are brought about, perhaps investigating in more detail how parental 'solicitude' (Daly & Wilson, 1980) varies as a function of sex and birth order.

Future research therefore needs to continue to develop good data collection and statistical techniques in order to fully control for confounding factors; to explicitly set up tests to distinguish between rival hypotheses for investment strategies; to focus more on identifying parental investment itself, rather than relying on child outcomes; to consider the mechanisms by which patterns of investment are brought about; and to do all this across a range of different environments and economies, in order to develop a full understanding of human parenting and family relationships.

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Box 7.1. The form of the human family.

The human family is a diverse entity. Humans cluster with their kin and their mate(s), who co-operate to varying degrees in the raising of children and productive work, but exactly how such families organise varies between populations. Some form of socially recognised union between a man and woman is pretty much universal across human societies, though the stability and the length of these unions differ. Most cultures worldwide allow polygynous marriage (one man married to several wives; (Murdock & White, 1969). A marital system of polyandry, one woman married to several husbands, is rare but has been observed in a handful of populations, and a polyandrous mating system may be much more common (Hrdy, 2000). Numerically, the most common form of marriage which currently exists is monogamy, since the rise of socially imposed monogamy in some of the dominant global cultures (MacDonald, 1995). Socially imposed monogamy is a form of marriage maintained by social pressures and rules, even where other marriage forms may be ecologically viable. Usually, these marriage systems will involve co-residence between husbands and wives, but some may in some societies involve visiting unions or living-apart-together relationships.

The nuclear family household, containing just a wife, husband and children residing in isolation from other kin, though the dominant family form in modern Western societies, is a rather rare family form. Instead, most couples will live with, or near, to either the wife's or the husband's relatives or both (the former is known as matrilocality or female-philopatry – females stay in the natal home; the latter known as patrilocality or male-philopatry). There is some debate in the literature about what 'ancestral' patterns of residence might be, since this may have an impact on the evolution of human social structure and other traits. There has been a long-standing view that residence patterns throughout most of our species' history have been patrilocal (Ember, 1978; Chapais, 2008). Early analysis of cross-cultural ethnographic data suggested most forager populations were patrilocal (Ember, 1978), but a careful reanalysis of these data found instead that not only was matrilocality much more common than had been believed, but also that forager residence patterns were very flexible (Alvarez, 2004). Foragers are mobile and can potentially move to reside with whichever kin are needed at any one time. In the early years of a marriage, at least, this residence often seems to be matrilocal, perhaps so that women have their own kin around to support them through the early, and difficult, years of childbearing (Blurton Jones et al., 2005).

The advent of accumulated resources associated with the emergence of agriculture does seem to have resulted in a shift towards higher levels of patrilocality (Hrdy, 2000). Where men need to defend resources this may be easier if they cooperate with their male kin. Genetic evidence confirms that, in our recent past, females seem to have dispersed more widely than males (Wilkins & Marlowe, 2006). Even in patrilocal societies, however, women may still have access to their natal kin during a marriage, since dispersal tends to be neither very long-distance nor irreversible. So the distinction between patrilocality and matrilocality may not be quite as stark as it seems. The overall picture of the human family is one of flexibility, both between and within populations.

Box 7.2. Are later-borns ‘born to rebel’? Birth order and personality differences

One of the more influential ideas in the birth order literature is that birth order affects personality, a thesis given an evolutionary framework by Sulloway (1996) in his book *Born to Rebel: Birth Order, Family Dynamics and Creative Lives*. Evidence has steadily accumulated that birth order affects career achievement since Galton first observed in the 19th century that eminent scientists were more likely to be firstborns (Galton, 1874). Subsequent sociological research has suggested a mechanism for this differential, which is that it is driven by personality differences between birth orders (Ernst & Angst, 1983). Sulloway’s thorough survey of historical revolutions and the men who were responsible for them concluded that these differences could be boiled down to the conservative nature of firstborns compared to their more rebellious younger siblings. He argued that scientific breakthroughs, for example, had largely been driven by later-borns, such as Charles Darwin, since they were more capable of ‘thinking outside the box’.

The evolutionary twist which Sulloway added was that these differences arise from sibling competition for parental investment. Children within the family all compete for parental resources, but because humans give birth to single children typically at several year intervals, the playing field is not level for sibling competition. Sulloway argued that children of different birth orders would therefore have to adopt different tactics for attracting parental attention. Early born children, with the advantage of being older, larger, and more cognitively advanced, could adopt a conservative niche within the family, emulating parental attitudes, while later-borns would of necessity be forced to adopt a different niche, involving more flexible and more risky behaviours, seizing opportunities for investment where they could. Salmon (1999, 2003; Salmon & Daly, 1998) has extended this research to examine variation in familial sentiment by birth order, arguing that middle-borns in particular, should be less family-oriented than first or lastborns, since middle-borns suffer the most sibling competition and the least parental investment.

Such research, while well-received within much of the evolutionary community, has been criticised for methodological flaws (e.g., see Townsend, 2000 and response: Sulloway, 2000). Sulloway’s work, for example, has been criticised for focusing on a rather biased sample of individuals (his survey of historically important figures is largely a survey of rich, white men) and also for not systematically taking into account differences between biological and ‘functional’ birth order (the latter describing children, for example, whose elder siblings died young so that they were effectively raised as the firstborn child, even if they were not in reality the first child to be born to their parents; Freese et al., 1999). What will matter for sibling competition is not the actual birth placement of each child, but the number and order of the siblings each child had during the period of parental investment.

The subsequent work by evolutionary psychologists such as Salmon similarly has methodological flaws. As with Sulloway's work, it extrapolates a supposedly human universal from a very biased sample: like much evolutionary psychology, it depends entirely on a non-random sample of college undergraduates. It also fails to control for potentially confounding factors, such as the age and residence of other siblings. Such methodological problems should not, however, be used to conclude that birth order has no effect on personality, or other traits for that matter. As described in the main text, there are sound evolutionary reasons why children of different birth orders should receive different levels of investment from parents. Instead, the reader should approach birth order research with appropriate caution, and judge each study on its own merits, including assessing whether it has satisfactorily dealt with potentially confounding factors.

Box 7.3. Why are sex ratios at birth male-biased in *Homo sapiens*?

On average, human sex ratios at birth (SRBs) are around 105 males to every 100 females. This male bias has traditionally been ascribed to Fisher's original idea that parental investment in sons and daughters must be equal, given that on average the reproductive value of a male and a female must be equal (Fisher, 1930). The typically higher male mortality throughout childhood means that the average son will receive lower investment than the average daughter, since he will be more likely to die before the end of parental investment. The slight male bias at birth adjusts for this shorter period of parental care for males so that overall investment in males and females is equal. This hypothesis assumes that the marginal value of investment to each sex is the same, however, which the Trivers-Willard hypothesis (TWH) states may not always be the case (though the TWH attempts to explain within-species biases in sex ratios at birth, not a population-level phenomenon). Despite long-standing interest in evolutionary biology, then, the male-biased SRB in our species is not yet fully understood (Lazarus, 2002). This problem with predicting population-level sex ratios in other vertebrate species (Frank, 1990) has led some to argue that predicting individual variation in SRBs is likely to be a much more productive approach (West et al., 2002; West & Sheldon, 2002).

Figure 7.1. Bars represent the percentage of studies in which the presence of that relative improved child survival, from a review of all studies which investigated the impact of particular relatives on child survival (Sear & Mace, 2008)

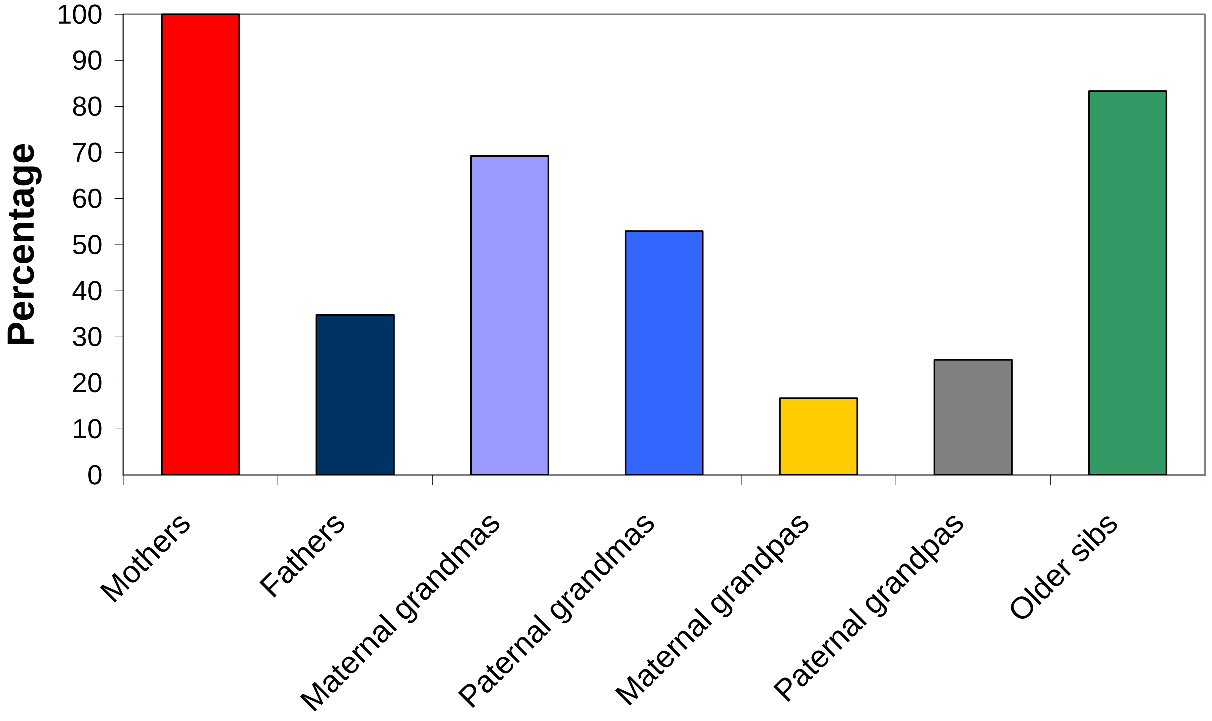

Figure 7.2. Reproductive value for women and men based on data from South Africa. From Bowles & Posel, 2005 (reproduced by permission of Nature Publishing Group).

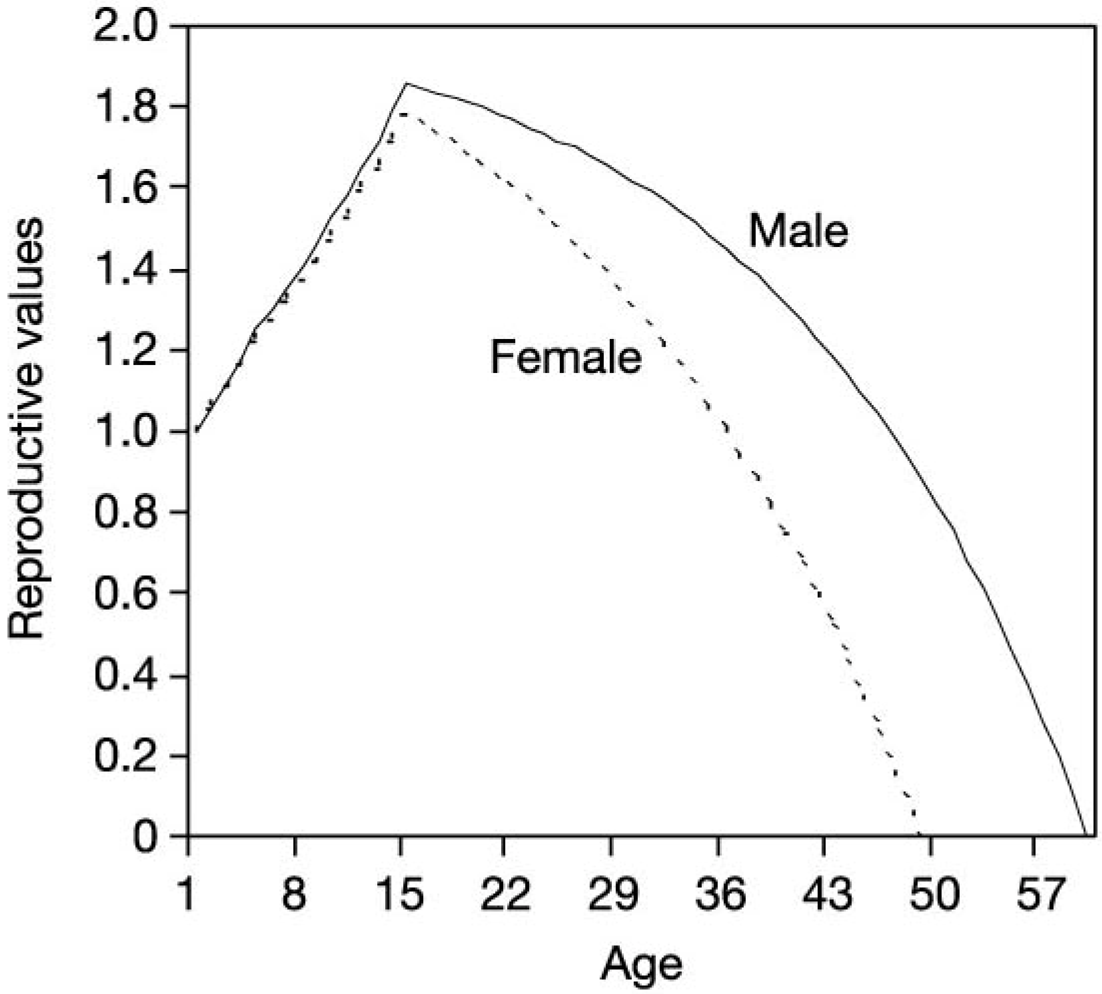

Figure 7.3. Spheres in the upper part of the figure represent resource allocation according to the equity heuristic as a function of birth rank in families with one, two, and three children. The bars in the lower part show the absolute and relative (i.e., calculated as a proportion of that for an only child) cumulative investments across four growth periods, or “years”). From Hertwig et al., 2002 (reproduced by permission of American Psychological Association).

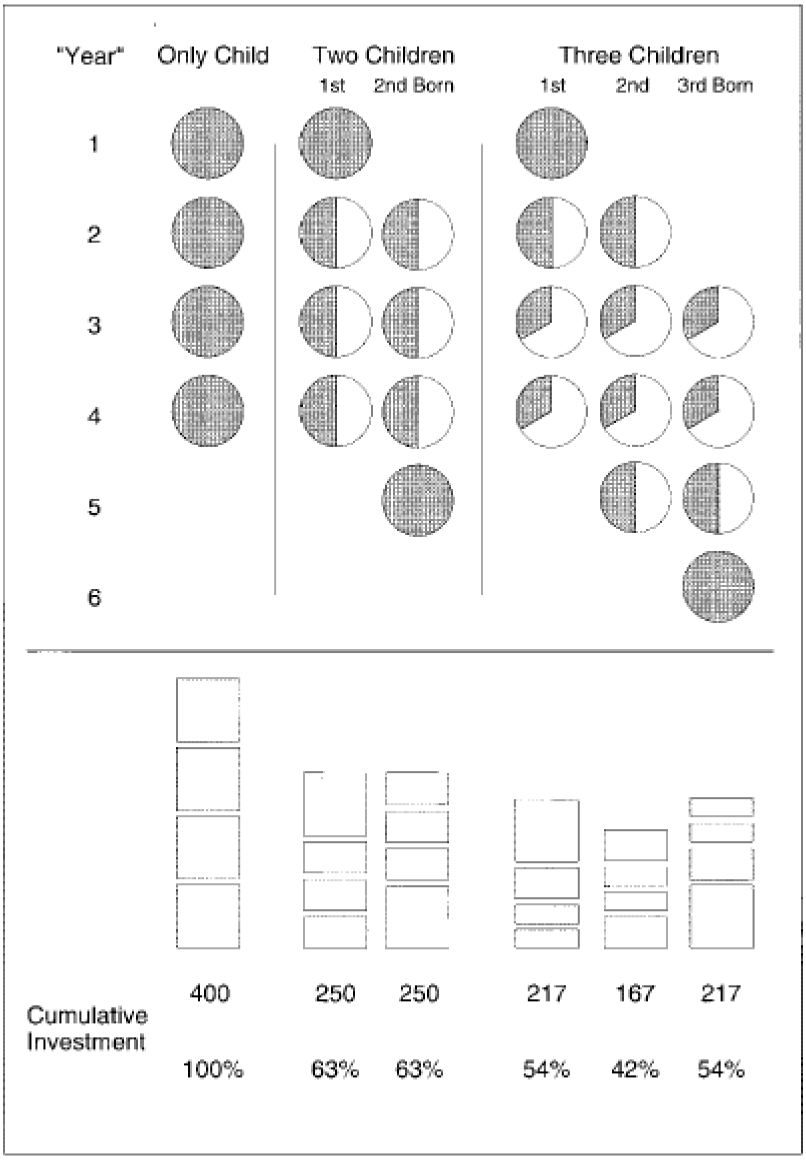

Figure 7.4. Schematic of the conditions necessary for the Trivers-Willard hypothesis: reproductive success of sons must be greater for parents in good condition but the reproductive success of daughters must be higher for parents in poor condition

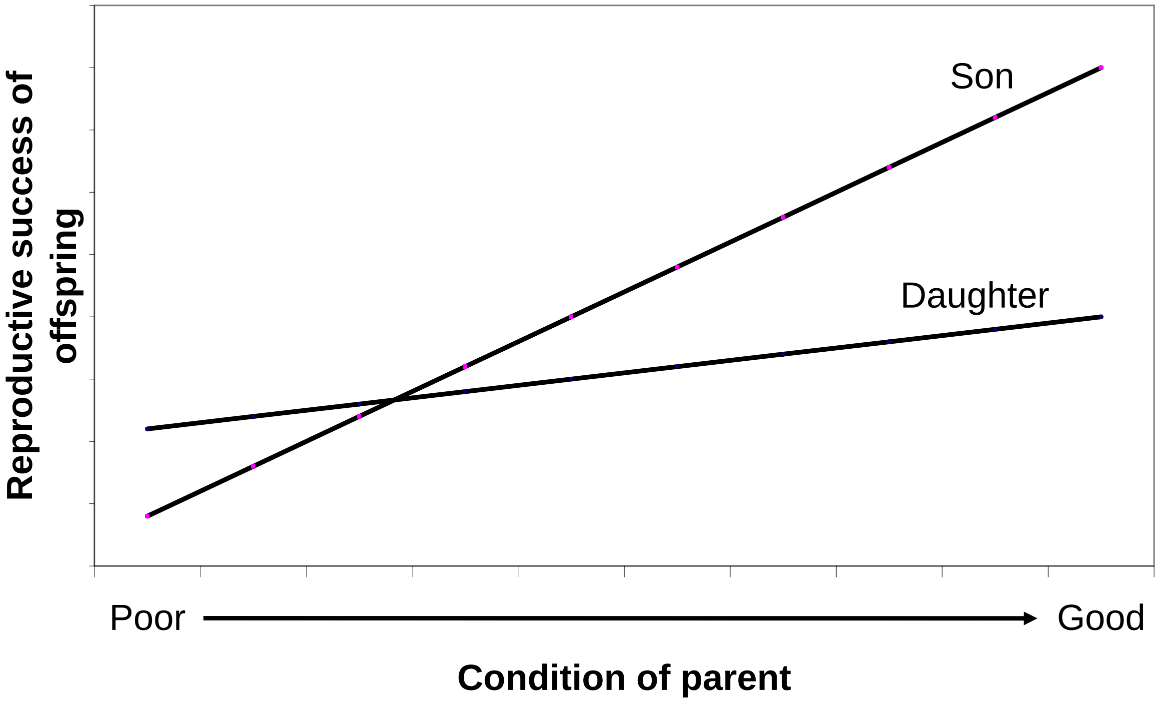

Figure 7.5. Higher sex ratio at birth in better nourished women in rural Ethiopia. From Gibson & Mace, 2003 (reproduced by permission of the Royal Society).