

Chapter 2

Our Children: Parental Decisions — How Much to Invest in Your Offspring

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Abstract Reproduction is the most fundamental of evolutionary behaviors, yet human parents face especially complex tradeoffs when deciding how many children to have and how much to invest in each of them. This chapter reviews parental investment theory, including both the key concepts and some important questions to which they have been applied in humans. Written primarily from the perspective of human behavioral ecology, this chapter also discusses how evolutionary social scientists have approached cross-cultural variation in parenting behavior. The chapter begins with an overview of life history theory and the concept of reproductive tradeoffs, focusing especially on the tradeoffs between current vs. future reproduction and quantity vs. quality of offspring. Discussing the critical question of who invests in offspring, I next compare motivations for investment between mothers and fathers, and explore the roles of many types of kin in investment, while considering whether humans can be viewed as cooperative breeders. I then explore the role of parent–offspring conflict and sibling conflict in parental investment and inheritance systems, followed by an exploration of sex biases in investment, including the Trivers–Willard effect local resource competition, and local resource enhancement. In conclusion, I argue that parental investment has been one of the most active areas of enquiry among evolutionary researchers over the last twenty years, and is likely to remain one of the mainstays of the field during the coming decades.

2.1 Introduction to Parental Investment Theory

How many children should parents have, and how much time and resources should they invest in each of them? These are the two central questions at the heart of evolutionary approaches to parental investment. Each question implies a tradeoff

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— the first between current and future reproduction, and the second between offspring quantity and offspring quality. The study of parental investment centers on the ways in which different ecological and cultural circumstances change the costs and benefits of investment, causing people to arrive at different answers to these two questions.

In his seminal 1972 article, Trivers defined parental investment as “any investment by the parent in an individual offspring that increases the offspring’s chance of surviving [...] at the cost of the parent’s ability to invest in other offspring” (Trivers 1972, p. 139). Other perspectives have expanded the concept to include many types of behavior which increase an offspring’s fitness while reducing the resources parents have to invest in other offspring, self-maintenance, future reproduction, or aid to other kin; the concept has also been extended to kin other than parents (Clutton-Brock 1991; Hamilton 1964).

Thus defined, parental investment includes most types of direct care, including gestation, lactation, food provisioning, protection, and the education/training of offspring. Complex human social systems also create opportunities for additional forms of parental investment not typically thought of as parental care, such as arranging marriages, transferring social connections, and endowing offspring with wealth (Alexander 1990; Trivers 1972). The benefits of parental investment to offspring can also take many forms, including effects on survival, growth, health, immune function, and social status, which ultimately affect fitness, the number of offspring (or other close kin discounted by their degree of relatedness) surviving in future generations.

The benefits provided to offspring, however, come at costs to parents. Time spent rearing offspring can lead to lost mating opportunities or a delay before parents can have another offspring, while resources spent rearing offspring can reduce the resources left for other offspring or impede a parent’s ability to repair and maintain their own body. Parental investment theory predicts that parents have been shaped by natural selection to maximize the difference between the benefits and the costs of parental investment, which they do by making tradeoffs in offspring number and/or the care that each offspring receives.

This chapter is written primarily from the perspective of human behavioral ecology (HBE), or human evolutionary ecology. Deriving from the study of animal behavior, HBE and HEE attempt to explain human behaviors as adaptive solutions to the competing demands of growth and development, knowledge and status acquisition, mate acquisition, reproduction, and parental care (Smith & Winterhalder 1992). HBE and HEE also aim to understand variation in human behavior both across and within human cultures.

This paper aims not only to introduce parental investment theory, but additionally to provide an overview of some of the many important questions and topics to which it has been applied in humans. I will begin with an overview of the classic theoretical insights that originated the study of parental investment, including life history theory and the concept of reproductive tradeoffs. I will then discuss the important issue of who cares for children, exploring the roles of parents and other relatives. Next I will discuss two key issues involving inequality in investment: parent–offspring and sibling conflicts, and sex biases and the Trivers–Willard effect. In each section I will explore some of the primary themes in the literature, introducing theory along with examples of relevant research.

2.2 Life History Theory and Tradeoffs

The evolutionary ecology perspective on reproduction is centered on the idea that human fertility and mortality decisions follow the patterns expected under life history theory, a branch of evolutionary biology that focuses on the relationships between growth, reproduction, and survival across the life cycle (see, e.g., Borgerhoff Mulder 1992; Chisholm 1993; Clarke & Low 2001; Hill 1993; Hill & Kaplan 1999; Low 1998; Mace 2000). Insights and predictions from life history theory bear directly on key questions about reproduction, including the timing of births, the number of offspring born, how much parents invest in children, and the relationship between mortality and fertility. Evolutionary researchers have applied this perspective to cultures in varying ecological circumstances and have found strong evidence for its utility in understanding and predicting both individual reproductive behavior and human population processes.

According to life history theory, an organism's lifetime is characterized by tradeoffs between investment in somatic effort and reproductive effort (Borgerhoff Mulder 1992; Chisholm 1993). Somatic effort is investment in development, growth, and maintenance of the body, while reproductive effort is investment in any aspect of reproduction; the latter is usually subdivided into mating effort and parenting effort (Alexander & Borgia 1979). Tradeoffs exist because any time or energy invested in one type of effort reduces the amount of time or energy that can be invested in the other. Lessels (1991) argues that many major life history tradeoffs can be subsumed into two categories relevant to reproduction:

- the tradeoff between current and future reproduction,
- the tradeoff between offspring quantity and offspring quality.

2.2.1 *Current vs. Future Reproduction*

Perhaps the most fundamental reproductive tradeoff is that between beginning reproduction and continuing investment in somatic maintenance, growth, development, and/or the acquisition of knowledge, status, or mates (Chisholm 1993). Generally, when mortality risks are high, organisms do better by maturing faster and reproducing early in life. This is because the longer an organism delays reproduction, the more it increases its probability of dying before it gets a chance to reproduce. When mortality is low, however, organisms can afford to delay reproduction and prolong somatic investment in the hope of greater reproductive success later in life.

An important concept in the study of this tradeoff is reproductive value (RV). Defined by Fisher (1958), RV is the number of offspring an individual of a given age can expect to produce in the remaining years of its life, adjusted by the probability of surviving each of those years. At any given age, reproductive value can be partitioned into current reproductive value and residual reproductive value or RRV (Williams 1966). Increasing or continuing investment in current offspring reduces

the resources available to future offspring, and thus RRV, whereas decreasing or withdrawing investment from current offspring increases the resources available to future offspring, increasing RRV.

For women, RRV increases sharply until around age twenty, at which point it begins to fall off quickly, reaching zero at menopause around age 50; for men reproductive value increases more slowly until the early 20s, then tails off more gradually, reaching zero around age 70 (see, e.g., Hamilton 1966). Very early reproduction can entail significant costs in terms of growth and development as well as the ability to invest later in life. For example, Nigerian women who had their first births as teenagers showed impaired growth compared to women who had later first births (Harrison et al. 1985). Alternatively, delaying reproduction too long can also entail costs in terms of both fertility (the number of children born) and fecundability (the ability to conceive). For example, highly educated women in modern developed nations often delay childbearing so long that they have significant problems with conception and childbirth, reducing fertility levels and sparking demand for medical technologies to treat infertility (Kaplan et al. 2002).

Because they do not undergo menopause, men can afford to delay reproduction longer than women without significantly reducing lifetime reproductive success. Moreover, in low mortality settings with large wealth differentials, delaying reproduction can increase male reproductive success if that time is used to increase wealth or status (Miller 2000). Females may also get some benefits from delay in societies where they also compete for wealth or status, but women face more serious fertility consequences, because delaying reproduction does not delay menopause or change the steep decline in RRV with age.

2.2.2 *Quantity vs. Quality*

The second fundamental tradeoff is between parental investment (the resources and care expended on each offspring) and fertility (the number of offspring born and reared) (Trivers 1972). High levels of parental investment in existing offspring necessarily require lower fertility, while low levels of parental investment in offspring allow for higher fertility.

MacArthur and Wilson (1967) defined two general strategies organisms can take in negotiating this tradeoff. An r-selected strategy occurs in unpredictable environments with high mortality rates, where it is important to reproduce quickly or risk not being able to reproduce at all; r-selected species have early ages at maturation, high fertility, and low levels of parental investment. In more stable populations which are nearer the carrying capacity (K) of an environment, however, within-species competition for resources increases. In these circumstances, natural selection favors organisms that have later ages at maturation and fewer offspring, but invest more heavily in each. Primates as an order are K-selected organisms, known for their high levels of parental investment. Most species of Old World monkeys and apes (our closest relatives) bear one offspring at a time, engage in a lengthy

period of lactation, and have relatively long interbirth intervals lasting from one to eight years (Alvarez 2000). Humans fit much of this pattern. We usually only give birth to a single offspring at a time, periods of breastfeeding last from 2–4 years in traditional societies, and children are not self-sufficient or productive foragers until well into their teens or even later (see, e.g., Borgerhoff Mulder 1992; Hill & Hurtado 1996; Kaplan 1996; Lee 1979). While the terms *r*-selection and *K*-selection are usually used to designate differences between species, they are sometimes applied to differences within species. For example, Wilson and Daly (1997) found that women in Chicago neighborhoods with high mortality rates had both higher fertility rates and earlier ages at first birth (and thus relatively more *r*-selective reproductive strategies) than women in neighborhoods with lower mortality rates.

Interbirth Intervals

In humans as in other species, the amount of time between the birth of one offspring and the next is one measure of parental investment. Longer interbirth intervals are generally associated with higher levels of parental investment or a more quality-oriented strategy, while shorter birth intervals are associated with a low parental investment and high fertility strategy (Borgerhoff Mulder 1992). Humans are unusual, however, in that we customarily have several dependent offspring at one time, meaning that short interbirth intervals may affect not only the most recent child but older children as well.

Humans in many foraging societies have moderate to very long interbirth intervals sustained by long periods of lactation and lactational amenorrhea (see, e.g., Lee 1979). For example, Lee finds that among the !Kung of the Kalahari Desert, interbirth intervals of nearly 4 years were sustained by women who faced the high workloads of active foraging, whereas interbirth intervals shortened by nearly a year when women settled on cattle stations and led more sedentary lives. In many cases the length of these birth intervals is positively associated with child well-being. For example, Blurton Jones (1986, 1987) found that, except for the first, shorter interbirth intervals were linked to higher rates of child mortality among the !Kung.

The same basic tradeoff holds among many non-foraging cultures as well. For example, Gibson and Mace (2006) found that an increase in birth rates caused by the introduction of wells into villages in Ethiopia was associated with decreased child nutritional status and higher mortality when siblings were very closely spaced. In two large comparative studies of 26 and 39 developing nations, Hobcraft, McDonald, and Rutstein (1985) found that birth intervals shorter than 2 years were associated with significantly higher risks of infant and child mortality than were longer birth intervals. Similar effects are also found in the developed world. Among women from the United Arab Emirates, short inter-pregnancy intervals were associated with preterm births, a significant risk factor for child mortality and developmental complications (Al-Jasmi et al. 2002).

Mortality and Risk

Quantity/quality tradeoffs are heavily influenced by mortality rates. In general, when mortality rates are high, natural selection should favor a strategy of higher fertility and lower parental investment, while when mortality rates are low, natural selection should favor a strategy of lower fertility and higher parental investment (Gasser et al. 2000). Chisholm (1993) argues that individuals who experience high mortality environments as children are more likely to reproduce early and often and invest less per child, while those who experience lower mortality environments are more likely to delay reproduction and pursue a strategy of lower fertility and higher parental investment (see also Draper & Harpending 1982).

When discussing on the effects of mortality on human fertility, some authors emphasize the difference between care-dependent and care-independent forms of mortality or, more generally, risk (see, e.g., Quinlan 2007). Care-dependent, or intrinsic, forms of risk can be reduced by the actions of parents or other caretakers. On the other hand, extrinsic or care-independent types of risk cannot easily be ameliorated by caretakers. High levels of intrinsic risk are predicted to lead to increased parental investment, while high levels of extrinsic risk should lead to lower levels of parental investment. Quinlan and Quinlan (2007) use parental investment data from the *Standard Cross-Cultural Sample* to argue that unresponsive parenting practices may be adaptive in high-risk environments, such as those associated with high levels of extramarital sex, aggression, theft, and witchcraft. Using the same data, Quinlan (2007) finds that the level of maternal care is inversely correlated with such extrinsic risks as famine, warfare, and high levels of pathogen stress.

Family Size

Some authors have attempted to demonstrate a quantity–quality tradeoff in particular human populations directly by comparing fertility and child survival to determine whether an intermediate number of children appears to be optimal. Blurton Jones (1987) finds that, among the !Kung foragers of the Kalahari desert, intermediate numbers of children are optimal with respect to child survival. Hagen et al. (2006) find that, among the forager–horticulturalist Shuar, children living in households with a higher consumer-to-producer ratio were shorter and had lower nutritional status. Shorter and lighter children are at risk of increased mortality and decreased fertility rates, suggesting that an intermediate number of offspring might be most likely to optimize long-term fitness in this population. And Strassmann and Gillespie (2002) find that large numbers of siblings are associated with reduced child survival among the agricultural Dogon of Mali, while an intermediate number of children is ideal.

2.3 Who Invests: Mothers, Fathers, Grandmothers, and Others

Investment in offspring can be provided by the mother and father, but also by other relatives and group members. The question of who cares for children has been the subject of a great deal of research in recent years, with attention being paid especially to two hallmarks of human investment behavior:

- non-maternal care,
- variations in patterns of investment between societies.

2.3.1 *Mothers and Fathers*

Drawing on seminal work by Bateman (1948) and others, Trivers (1972) argued that, within species, the sex which invests more heavily in offspring will become a limiting resource for the other sex. Among mammals, the higher investing sex is most often females since they bear a much larger burden of obligatory parental investment (Clutton-Brock 1989). Among humans, for example, the minimum amount of male parental investment is the sperm necessary for conception. For women, in contrast, the minimum amount of parental investment required is the much larger egg cell, 40 weeks of gestation, and a period of lactation that in traditional human societies can last for several years. This suggests that, in general, humans should follow the stereotypical pattern of high female parental investment and male competition for choosy females.

Yet levels of parental investment vary significantly both between and within species, and humans are a highly variable species in terms of male and female contributions to parental investment (see, e.g., Brown et al. 2009; Hill & Kaplan 1999; Voland 1998). In fact, Trivers' model predicts that, in species with high paternal investment, females should compete for access to males since it is male investment which may be the limiting factor on female reproductive success (Trivers 1985). Moreover, Brown et al. (2009) argue that a careful reading of Bateman's principles and cross-cultural comparison of human mating and population structures shows that, since human cultures vary in characteristics such as population density and sex ratio, Bateman gradients should differ between human populations. The authors find that, while men on average have greater variance in reproductive success than women, suggesting that men should compete for women who invest more, this is not always true. Moreover, though monogamous societies generally have smaller differences between male and female RS than polygynous ones, indicating a greater motivation for male parental investment in monogamous groups, there is tremendous variation across both polygynous and monogamous societies.

One thing that varies little, however, is that mothers are the most important caretakers of young children in most human societies. For example, in a recent review article entitled *Who keeps children alive?*, Sear and Mace (2008) found that mothers have a virtually universal — and often profound — positive effect on child survival,

while maternal death is often associated with extraordinarily high rates of mortality for young children. Since maternal care is so pervasive, it shows less cross-cultural variability than care by other kin or group members. Yet how and how much mothers invest does vary between societies and individuals, often in ways that are consistent with levels of resources, risk, and opportunity costs (Hrdy 1999; Voland 1998). In general, mothers who are healthy, have abundant resources, face lower opportunity costs, have fewer helpers, or expect high returns on parental investment invest more per child, while mothers who are less healthy, lack resources, face greater opportunity costs, have more helpers, or expect low returns on parental investment may choose to limit investment per child or terminate investment in particular children entirely (Hrdy 1992; Kaplan 1996; Trivers 1974; Trivers & Willard 1973).

While human mothers perform the bulk of care for infants and children, humans are unusual among higher primates (monkeys and apes) for the high amount of investment in offspring by fathers (Marlowe 2000). Investment by fathers has long been touted as one of the hallmarks of the human species, and the importance of fathers in provisioning and/or protecting mates and children has figured prominently in many conceptions of human evolutionary history (see, e.g., Lee & DeVore 1968). Both classic and recent models suggest that paternal aid in the provisioning and care of children has helped to fund the high reproductive rates of humans as compared to other primate species (Kaplan et al. 2000; Marlowe 2000). Some also argue that paternal investment is a key to the development of important human cognitive and social abilities (Flinn et al. 2007; Geary 2000; Hrdy 2009). While there is disagreement about just how important paternal investment has been in our evolutionary history, most researchers agree that our capacity for high levels of paternal investment is a key evolved feature of human behavior.

Among the highest levels of direct paternal investment are found among the Aka peoples of the Central African Republic. In these groups, fathers spend a great deal of time holding infants and playing with young children, in some cases nearly rivaling the time spent by mothers (Hewlett 1991). The same pattern appears to be found in many other forager groups as well (Marlowe 2000). Fathers also appear to be highly important in monogamous societies with high levels of parental investment, such as modern nations in Europe and North America (Harrell 1997; Marlowe 2000). In other cases — most frequently among horticulturalists — the role of fathers is more flexible, with fathers being key players in some families but not others (Leonetti et al. 2007; Marlowe 2000).

There are other cases in which fathers appear to be less important or even uninvolved. Sear and Mace (2008) find, for example, that in over half of the societies for which they had good data, fathers had no effect on child survival. In contrast, Scelza (2010) suggests that the limited importance of fathers found in some societies may be an artifact of the measures commonly used as indicators of investment, including child mortality and child nutritional status, which may underestimate the importance of fathers if their contributions come later in the life cycle, during adolescence or adulthood. For example, Scelza (2010) finds that adolescent Martu aborigine boys with an absent father or father figure have delayed age at initiation and consequently delayed age at first birth.

2.3.2 *Grandmothers and Others*

Humans show evidence of a great deal of alloparenting, or care given by people other than the parents, especially in traditional societies (Hrdy 2009; Mace & Sear 2005). The complexity of human social systems also allows for a great deal of variation between societies — far more variation than is common among other primates. Recent work has emphasized the importance of grandparents, aunts and uncles, siblings, and occasionally others in keeping children alive and improving their prospects for finding mates and reproducing.

Most famous of the perspectives on the contribution of non-parental kin has been research on the importance of grandmothers. Based on their work among the Hadza foragers of Tanzania, Hawkes and colleagues (1997) developed the ‘grandmother hypothesis’ as an explanation for the evolution of menopause in humans. Menopause is a very rare event among animals, and its origins are hotly debated. Hawkes et al. argued that humans evolved the ability to have multiple dependent offspring at one time because the additional work it took to provision and care for simultaneous children was subsidized by post-menopausal women working alongside their daughters or daughters-in-law to feed and care for their grandchildren. The crux of this model is the suggestion that older women get a better reproductive payoff by investing in grandchildren than they would get from continuing personal reproduction into an increasingly feeble old age.

The grandmother hypothesis has been both influential and controversial (see, e.g., Voland et al. 2005). An alternative perspective is provided by Williams (1957) who suggested that, given the very long dependency periods of human children, it was just as likely that women ceased reproducing in order to successfully rear their own offspring to adulthood. Others have argued that menopause is better understood as a result of the biology of human ovaries, which are optimized to maintain regular cycles at young ages (see, e.g., Wood et al. 2001). Despite these critiques, a great deal of work has been done by numerous researchers to test the implications of the grandmother hypothesis in societies around the world (Voland et al. 2005). These results can best be described by revisiting the review article by Sear and Mace (2008), who find substantial cross-cultural support for the importance of grandmothers (though their impact is not always positive), but also for the importance of other relatives (including fathers, sisters, aunts, and occasionally grandfathers) as well as a great deal of variation between societies in terms of which relatives helped or hurt children’s survival. This work suggests that, while grandmothers can be very important, they are not universally or uniquely so.

Various authors have considered the importance of siblings to parental investment. Kramer and Boone (2002) argue that high fertility among intensive agriculturalists is underwritten by the labor of children on the farm. Using data on Maya children in rural Mexico, they show that, while children may not be self-sufficient at early ages, the work they do reduces the workload of their parents, freeing up time and calories that can be spent on subsequent reproduction. Kramer (2005) further argues that partial self-provisioning by children is common in traditional societies following many subsistence patterns (hunter–gatherer, pastoralist, agricul-

turalist) and contributes to the human capacity for high reproductive rates. Other ways that siblings can be important are considered in Sect. 2.5.

Several studies have also examined the effects of investment by aunts and uncles. In a study of US college students, Gaulin et al. (1997) find that, while aunts generally invest more than uncles, maternal relatives invest more than paternal relatives; they interpret this outcome in terms of the greater risk of paternity uncertainty on the part of patrilateral relatives. Similar results were found by Pashos and McBurney (2008). Shenk (2005) found that the education and wealth of aunts and uncles had a positive effect on children's education and income, but that the numbers of aunts and uncles had a negative effect. Sear and Mace (2008) also report uneven results for the effects of aunts and uncles on child survival, with positive and negative effects of both aunts and uncles in several historical or traditional populations.

Human societies are also unusual in that they regularly engage in the adoption and fostering of children. These practices are especially common in traditional societies in Africa and Oceania, but are nearly universal in some form among human groups (see, e.g., Harrell 1997). Some authors have argued that these customs, especially where they are common, are probably related to the need to adjust the number or genders of dependents between households, as either too few or too many may cause resource stress and lead to inadequate provisioning or care of children (Harrell 1997; Silk 1980; Turke 1988). As predicted by the principle of kin selection (Hamilton 1963), in traditional societies adoption and fostering are most common among close kin.

2.3.3 Are Humans Cooperative Breeders?

The importance of relatives to the care of children in so many societies, combined with cross-cultural diversity in terms of whom the key relatives are, has caused several authors to draw the conclusion that humans should be characterized as cooperative breeders (Hrady 2009; Kramer 2005; Mace & Sear 2005; Sear & Mace 2008). Kramer (2005) and Sear and Mace (2005) argue that our history as cooperative breeders is the best explanation for the high rates of fertility in humans, as compared to our close primate relatives. Hrady (2009) further contends that cooperative investment has been a key in the evolution of our psychological adaptations for empathy and cooperation, which are unique among animals.

While many authors have come to question Hawkes et al.'s (1997) perspective on the primacy of grandmaternal investment, there is increasing agreement that cooperative breeding strategies (of which grandmothers are in many cases a key part) are in fact related to the evolution of menopause (Sear & Mace 2005). Early attempts to model or predict menopause suggested that the inclusive fitness benefits of mothering or grandmothering were not sufficient to offset the potential benefits of continuing to reproduce (Hill & Hurtado 1991, 1996; Rogers 1993). Cant and Johnstone (2008), however, argue that if one takes the costs of reproductive competition into account, one reaches a different conclusion. They argue that, in the

context of female dispersal, which likely characterized early human societies, older women will compete with younger, immigrant women who have a competitive advantage, because they are insensitive to the reproductive costs of older females and have less to gain from cooperation. In these circumstances, the benefits of continued reproduction may become low enough that there would be selection for reproductive cessation. If post-menopausal women are able to focus investment on older children and grandchildren, this would only strengthen the benefits of cessation.

2.4 Parent–Offspring and Sibling Conflicts

Reproducing and investing in offspring is enormously costly in terms of time and other resources. Individuals are limited in the amount of energy they can devote to producing and raising young, and such expenditures may be detrimental to the investor's own condition, survival, and future reproductive output. However, investment is typically beneficial to the offspring themselves, enhancing their condition, survival, and reproductive success. These differences in the perspectives of parents and offspring may come into conflict at times, leading to what Trivers (1974) referred to as parent–offspring conflict. Such conflicts can begin very early in pregnancy, continue throughout infancy and childhood, and in some circumstances extend through the marriage of a child or the division of parental resources among children. A closely related type of conflict occurs between siblings when they compete with each other for access to resources or mates (see, e.g., Trivers 1974, 1985). As with parent–offspring conflict, sibling conflict often begins at young ages, but in humans can extend throughout the lifespan. This section will cover two key types of parent–offspring and sibling conflicts; there are many others which I do not have space for here.

2.4.1 Infanticide and Neglect

Human parents often have to make difficult decisions about how to divide resources between existing older offspring, new infants, and potential future offspring. One of the most widely studied examples of how parents manage this tradeoff is infanticide, a phenomenon which exists in some form in many animals, including many species of primates and most human societies (see, e.g., Daly & Wilson 1988; Hrdy 1992). In a survey of the infanticide literature, Daly and Wilson (1988) found that most human infanticide is attributable to one of three circumstances: poor offspring quality, lack of parental resources, or lack of certainty regarding paternity. Each of these has clear evolutionary implications. Research on the non-lethal neglect of children often shows similar patterns.

Lack of parental resources commonly affects fertility and parental investment decisions in two ways. First, younger women may use infanticide or neglect to delay

childbearing or investment until they are in more favorable circumstances. Second, older or poorer women may use investment or neglect as a means of protecting their investment in existing children, as large numbers of children or closer birth spacing can increase the level of competition between siblings and put the investment already made in older offspring at risk. For example, both types of motivations can be found for abortion in modern Western societies. Young, unmarried women are often the most common abortion patients, especially when they do not have a supportive partner or they feel as though having a child would put their education or job opportunities at risk (Finer et al. 2005; Hill & Low 1991; Lycett & Dunbar 1999). Women in their 30s or older, on the other hand, usually cite poverty or responsibilities to older children as their primary reasons for seeking an abortion (Finer et al. 2005). Many authors have found that abortion rates among single women drop as they become older, and argue that, as the likelihood of finding a better future circumstance for childbearing becomes lower, current reproductive effort becomes more valuable than future effort (Hill & Low 1991; Lycett & Dunbar 1999; Tullberg & Lummaa 2001).

Children with physical deformities or mental handicaps are at high risk of abuse, neglect, and infanticide cross-culturally (Daly & Wilson 1984). If parents are poor enough, even more subtle signs of low infant quality such as listlessness or failure to thrive may be cues that cause parents to limit investment. In the poor shantytowns of Northeast Brazil, for instance, Scheper-Hughes (1992) describes maternal decision-making in the context of extreme poverty and very high infant mortality rates. Instead of investing more in children who appeared weak or sick, mothers often reduced investment and instead targeted care and resources towards infants who showed higher energy levels and greater frequency of crying — infants they interpreted as more likely to survive and/or thrive in their challenging environment.

Twins are also at higher risk of infanticide cross-culturally (Ball & Hill 1996). Twins are problematic for two reasons. First, twinning is associated with prematurity, low birth weight, and occasionally other developmental anomalies, all of which may put children at risk of higher mortality as well as physical and mental problems at later ages (Ball & Hill 1996). Second, in many traditional cultures it is difficult for mothers or their kin to provide sufficient breast milk or care for two infants at the same time, thus imposing stress on children and families which can lead to problematic outcomes. For example, in 18th and 19th century Germany, Gabler and Volland (1994) found that both twins and their mothers suffered higher mortality rates than women who had single children, and that women who had twins paid a fitness cost in terms of lower numbers of surviving grandchildren. While Sear et al. (2001) found that in Gambia mothers of twins had more surviving children, this was despite the much higher rates of stillbirth and neonatal mortality among twins as compared to singletons.

Paternity certainty is an important evolutionary consideration since in many societies men may limit or terminate investment in offspring they believe are not their own. In a cross-cultural analysis of infanticide using the 60 societies in the *HRAF Probability Sample*, Daly and Wilson (1984, 1988) report non-paternity as a reason given for infanticide in 20 societies with specific concerns ranging from adulterous

conceptions (the most common), to non-tribal sires, to the fact that the children were from a woman's first marriage. Furthermore, Fuster (1984) finds that mortality rates were much higher for illegitimate than for legitimate infants in late 19th and early 20th century Galicia, and were especially high among children not recognized by either the mother or the father.

2.4.2 Differential Investment and Inheritance

Parent–offspring and sibling conflicts are especially common in societies where wealth, often in the form of animals or land, is inherited. In such circumstances siblings of one or both genders directly compete for familial resources which are limited in size and may not be easily divisible. A certain number of cows or amount of land, for instance, usually needs to remain intact in order to support a family. In some situations these kinds of constraints may lead parents to adopt restricted forms of inheritance such as primogeniture, where the oldest child (usually the oldest son) inherits most of the family property, or ultimogeniture, where the youngest son or daughter inherits most of the family property.

Among the Gabbra pastoralists of East Africa, Mace (1996) found that later-born sons married at older ages, were given smaller herds on marriage, and often had lower fertility than their older brothers. She argued that this was likely a deliberate strategy on the part of parents to make sure that some sons would be successful; alternatively, it could be viewed as a the result of competition among siblings which older sons are better positioned to win. Low (1991) found a similar effect in 19th century Sweden, in which the presence of older brothers reduced the fertility of younger brothers. Volland and Dunbar (1995) found similarly that, among 18th and 19th century land-owning farmers in the Krummhörn region of Germany, later-born sons and daughters had higher infant mortality rates than their older same-sex siblings; these relationships did not hold true among landless laborers in the same area, suggesting that sibling competition may be stronger in groups with heritable wealth. Celibacy was also a common practice in some agricultural societies of Europe and Asia where wealth was based on land ownership. Many families only allowed one son and one daughter to marry in each generation, while their siblings stayed home to help with the farm or migrated to find work elsewhere (Boone 1986; Hajnal 1965; Deady et al. 2006).

Such tradeoffs are also present, if not more exaggerated, in modern industrial environments. For example, Kaplan (1996) argues that in modern wage-labor economies with education-based job markets, fertility has the potential to reach very low levels because the perceived payoffs to parental investment do not diminish until very high levels. He also argues that this calculus is stronger for more highly-educated people since they are more efficient at investing in education for their own children, leading to very high levels of investment as well as an inverse relationship between wealth and fertility. Similarly, Lawson and Mace (2009) find that, in contemporary Britain, children from smaller families received more investment per

child than children from larger families, even when the effects of wealth were adjusted for, and, moreover, that the effects of the tradeoffs were more negative for later-born siblings. They also found that, as parents became wealthier and better educated, the strength of the tradeoffs increased.

2.5 Sons vs. Daughters: Sex Biases in Parental Investment

Interest in the evolutionary relationship between parental investment and offspring sex began with Fisher (1930), who argued that, since sons and daughters receive equal genetic contributions from both parents, investing in one sex will, on average, yield the same effect on parental fitness as investing in the other. An interest in sex-biased investment began when Hamilton (1967) suggested that, when siblings of one sex compete with each other for mates, parents may benefit by producing more of the opposite sex. Perhaps the best-known perspective on sex bias in parental investment comes from the 1973 *Science* article by Trivers and Willard, who argued that parents should bias investment towards the sex of offspring with the greatest potential for reproduction. In situations where the variance in reproductive success is higher for males than for females (which is usually the case in mammals), their model predicts that parents in good condition should invest more heavily in sons to take advantage of their higher potential RS, while parents in poor condition should invest more heavily in daughters because they are more assured of reproducing.

Predictions from these models have been tested many times in human populations. Human cultures, however, vary in multiple ways that change the payoffs to parental investment to either favor or discourage gender biases in investment. We thus see a wide variety of gender-biased investment strategies in response to varying ecological and social conditions.

2.5.1 The Trivers–Willard Effect

There are many cultures in which parents have been shown to systematically bias investment towards one sex or the other based on parental characteristics such as health, wealth, or social status. Sex-based investment can take many forms, from alterations of the sex ratio itself through infanticide or abortion, to mild or extreme forms of neglect, discrimination or favoritism, to investing different types of resources or employing different strategies in raising and marrying sons vs. daughters.

Evidence of son-biased investment is typically found among high status families or social groups. For example, daughters in elite families in traditional North India and China were often subject to infanticide because their marriage prospects were limited by rules of hypergyny dictating that women marry men of the same or a higher social rank. Daughters of high-ranking families faced a circumscribed marriage market because there were few places for them to marry upwardly, whereas sons of

elite families had good marriage prospects among lower-status women and in some cases were able to take multiple wives and/or concubines (Dickemann 1979). Similarly, several studies find that high-status fathers have more sons than average in modern environments (see, e.g., Cameron & Dalerum 2009; Hopcroft 2005). Hopcroft (2005) shows that sons of high-status fathers achieve more education than their sisters, while daughters of low-status fathers achieve more education than their brothers. Cameron and Dalerum (2009) argue that the high proportion of sons born to male billionaires compared to the general public is an adaptive strategy because the same population also leaves more grandchildren through sons than daughters.

In contrast, other groups show systematic evidence of daughter bias. For example, among the polygynous, pastoralist Mukogodo of Kenya, daughters receive more frequent breastfeeding and better medical care than sons because they have better marital prospects than their brothers, who are not sought after as husbands due to their low social position (Cronk 1991). Mukogodo men have lower rates of polygyny and lower reproductive success than Mukogodo women, making investment in daughters an adaptive strategy. Boone (1986) finds that, in medieval Portugal, daughters of the lower nobility had more children than their brothers, causing a shift in the investment of parental resources towards dowering daughters and helping to ensure that they married into high-status families. Finally, in their work on Hungarian Gypsies, Bereczkei and Dunbar (1997) show evidence for a female-biased sex ratio, higher investment in daughters, and a greater number of grandchildren through daughters than sons among urban Gypsies. Gypsies are at the lower end of the Hungarian socioeconomic spectrum, and girls have a much better chance to marry upwards than do boys. In response to this, Gypsy mothers breastfeed their daughters longer, are more likely to terminate a pregnancy after a daughter than a son, and pay for daughters to continue longer in school than sons.

2.5.2 Local Resource Competition and Enhancement

Two special cases of sex-biased investment take place when children of one sex either compete or cooperate with each other — or with their parents — in terms of subsistence or reproduction. Local resource competition occurs when children of one sex compete with each other or with their parents for the same types of resources, prompting parents to limit investment towards the competing sex in favor of the non-competing sex (Clarke 1978; Silk 1983; van Schaik & Hrdy 1991). Competition can occur over subsistence resources like food, heritable resources like land, or access to mates or mating opportunities. For example, Volland et al. (1997) compared six populations in early 19th century Germany and found that infant mortality rates for daughters were higher in areas where populations were increasing, while infant mortality rates for sons were higher in areas where populations were stable. The authors argue that sons could start new farms in unoccupied land, but once land ownership was saturated, sons competed with each other for land. In early modern Portugal, younger sons of noble families did not inherit the family estate but had to

work for status and wealth in the army or trade. Boone (1986) found that, among the high nobility, younger sons had much higher mortality and lower fertility rates than older, inheriting sons. He also found that this difference became more pronounced as Portugal's land became more saturated and estates became fixed.

Local resource enhancement occurs when one sex aids parents in reproduction (Emlen et al. 1986; Gowaty & Lennartz 1985) or offspring of one sex enhance the mating success of parents or siblings (Sieff 1990). In such circumstances, parents will be motivated to invest relatively more in the enhancing sex. For example, Turke (1988) reported that, on the Micronesian atoll of Ifaluk, women with first-born daughters had on average 2 additional offspring compared to women with first-born sons; this effect was significantly enhanced when comparing women whose two first-born children were daughters (who averaged 8.9 surviving offspring) as opposed to women whose two first-born children were sons (who averaged 5.1 surviving offspring). Berezkei and Dunbar (2002) found a similar trend among Hungarian Gypsies, where mothers with first-born daughters had shorter birth intervals and longer reproductive careers than mothers with first-born sons, leading to an average of one additional surviving offspring. This phenomenon, which was first described in birds, is often called 'helping-at-the-nest' (Emlen et al. 1986).

2.5.3 Marriage Payments as Sex-Biased Parental Investment

Marriage payments are common in human societies. Though there is variation in terms of the content of the payment and who pays whom, virtually all forms of marriage payments are sex-biased: they are given to one sex but not the other, or given to sons and daughters in different amounts (Goody & Tambiah 1973; Harrell 1997). Additionally, marriage payments can often be viewed as forms of parental investment because they serve to ensure a suitable marriage partner for a child who will also serve as an important source of investment in grandchildren (Shenk 2007).

The two primary forms of marriage payments are bridewealth, which is paid by the groom or his family to the parents of the bride, and dowry, which is paid by the family of the bride to the new couple or the parents of the groom (Goody & Tambiah 1973). From the perspective of parental investment theory, bridewealth makes daughters cheaper to raise because parents expect to gain from their marriages, whereas dowry makes them more expensive. In bridewealth systems, sons compete with each other, and in polygynous societies with their fathers, for access to the animals or other resources needed to pay bridewealth; in dowry systems, daughters compete with each other and with other family expenditures for the wealth needed to pay dowry.

Among the Kipsigis agro-pastoralists of Tanzania, Borgerhoff Mulder (1998) finds a pattern of same-sex competition and opposite-sex cooperation with regard to marriage payments. Parents use the bridewealth gained from daughters to help fund the marriages of their brothers, so there is competition among sons for bridewealth payments. Later-born sons with many brothers marry at older ages, wed

less preferred spouses, make lower bridewealth payments, and have fewer surviving offspring than sons with fewer older brothers, independently of family wealth. In contrast, sons with many sisters do better on all of these measures. Women do not show such tradeoffs with their sisters. In modern India, in contrast, the necessity of paying large dowries for daughters is often cited as a reason for neglect of higher-birth order daughters, whereas sons are more highly valued because of their ability to earn income, care for parents, and gain dowry (Shenk 2007). Both the Kipsigis and Indian cases provide examples of local resource competition and local resource enhancement operating simultaneously.

2.6 Conclusions

This chapter has reviewed the basics of parental investment theory, including some of the key questions to which it has been applied in humans, but it has barely scratched the surface of the literature on this topic. The study of parental investment has been one of the most active areas of enquiry among evolutionary researchers during the last twenty years (Smith & Winterhalder 2000). The reasons are quite simple: reproduction is the most fundamental of evolutionary behaviors, yet human parents face especially complex tradeoffs when deciding how many children to have and how much to invest in each. The wide variety of ecologies and economic systems in which humans live, coupled with the complexity of human social systems, results in a multitude of behavioral options for individuals. Straightforward rules of optimization, such as investing more in the sex of offspring that is likely to have more children, lead to a great deal of variation in observed behaviors across different types of societies and the different social strata within them. When coupled with other sources of variation, such as different marriage systems and the presence or absence of heritable wealth, the potential complexity of human parental investment behavior can seem staggering.

Yet finding simple rules to explain complex behaviors is a hallmark of the evolutionary ecology approach (Smith & Winterhalder 1992), and evolutionary researchers have made great progress in understanding many of the topics discussed in this chapter. Nonetheless plenty of unanswered — or partially answered — questions remain. For instance, many authors have recently emphasized the importance of conflict among kin to understanding parental investment (see, e.g., Borgerhoff Mulder 2007; Lawson & Mace 2009; Leonetti et al. 2007). There has also been a recent resurgence of work on the demographic transition emphasizing cultural influences, risk, and comparative research (see, e.g., Richerson & Boyd 2005; Shenk 2009; Winterhalder & Leslie 2002). New areas of enquiry, such as the study of arranged marriage as a form of parental investment and a site for parent–offspring conflict, are emerging (see, e.g., Apostolou 2007; Buunk et al. 2008). In the last few decades, evolutionary research on human behavior has become more methodologically rigorous, moving from descriptive work to complex simulations and statistical analyses. The number of researchers doing evolutionary work, and the number of

cultures they study, has also increased rapidly. As has been true in the past, however, the study of parental investment is likely to remain one of the mainstays of evolutionary approaches to human behavior for many years to come.

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