

Parent–Child Relationships

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Abstract

The chapter provides an integrative framework for the evolutionary analysis of parent–child relationships. Starting from basic concepts in life history theory, the chapter examines the effect of ecological factors on parent–child relations and discusses how parents modulate their levels of investment depending on children’s characteristics such as sex, age, and physical similarity to the father. Next, the chapter explores children’s provision of care and resources, the possibility of exploitation by parents, and cross-cultural variation in children’s role in the family. The final section introduces genomic imprinting and discusses how conflict between maternal and paternal genes can affect child development and parent–child relations.

Keywords: Attachment, caregiving, differential susceptibility, father-child resemblance, genomic imprinting, helping, life history strategy, parental investment, plasticity, sex-biased investment

Introduction

Few topics in psychology can rival the emotional appeal of parent–child relationships. At the same time—and perhaps for the same reasons—few areas of psychology cling so strongly to a romanticized view of human nature. Most of current developmental psychology is based, implicitly if not explicitly, on the idea that parent–child relationships are designed to be invariably fulfilling, maximally cooperative, and virtually free of conflict. Deviations from this ideal are usually treated as manifestations of individual or social pathology.

And this is exactly why the evolutionary approach to the family is so revolutionary: Biology shatters this romantic worldview at its foundations, by making conflict an essential and unavoidable feature of family relations (Trivers, 1974; see Chapter 6 by Salmon and Malcolm). This is possibly the single most important contribution of evolutionary biology to the study of families, as it illuminates and enriches our understanding of virtually all the processes

involved in parent–child, spousal, and sibling relations. However, despite the 35 years since Trivers’ (1974) landmark paper and a number of key evolutionary-oriented publications in leading developmental journals (e.g., Belsky, Steinberg, & Draper, 1991; Bjorklund & Pellegrini, 2000), developmentalists remain perhaps the most recalcitrant psychologists when it comes to embracing an evolutionary mindset. This is unfortunate, because what emerges from the evolutionary approach to the family is not a gloomy mirror image of the romantic worldview; rather, parent–child relations are revealed to reflect a fascinating and complex game, the central rules of which involve cooperation *and* conflict, positive *and* negative emotions, and a continuum of adaptive strategies instead of pervasive dysfunction. It is the rules of this game that are the focus of this chapter.

Affective Dynamics and Investment Dynamics

There are two basic ways to look at parent–child relations. One is to focus on what could be labeled

“affective dynamics”—the emotional, communicative, and affiliative processes that take place between parents and children. This is the traditional focus of developmental research, and is currently best represented by work informed by attachment theory (Cassidy & Shaver, 2008). Attachment theory was originally developed with a strong biological and ethological basis (Bowlby, 1969/1982, 1973, 1980), although it drifted away from biology as it entered the mainstream (but see Belsky, 1997a; Chisholm, 1999; Del Giudice, 2009; Ein-Dor, Mikulincer, Doron, & Shaver, 2010; Simpson & Belsky, 2008). On another level, parent–child relationships may be understood from the perspective of “investment dynamics”: In the ultimate sense, the biological function of parental care is to provide food, protection, shelter, and information (e.g., teaching of social and practical skills) to children. Parental investment results in a net fitness cost to the parent and a net fitness benefit to the child (for a more technical treatment of parental investment in human families, see Sear, in press).

These two levels of analysis are fully complementary: Investment dynamics underlie and motivate affective dynamics, and are the ultimate reason for their evolution. A child’s motivation to maintain closeness to his or her mother, the fear, protest, and despair if the mother is not there, and the sense of comfort that arises when in the arms of a loving parent are all crafted by natural selection to ensure parental investment—both in the here and now (e.g., protection from a possible danger) and in the future (by fostering mutual affection and love). Evolutionary biologists and psychologists use the analysis of investment dynamics as a tool to explain, understand, and predict the working of affective and behavioral dynamics. This approach has yielded a number of crucial insights into the psychology of parent–child relationships, some of which overlap with traditional theories, although others are novel and, in some cases, highly counterintuitive.

Overview of the Chapter

The aim of this chapter is not to provide a comprehensive treatment of the psychological processes involved in parent–child relationships. Rather, we offer the reader an integrative conceptual framework for thinking about parents and children from a modern evolutionary perspective. The unifying theme of the chapter is that of investment dynamics; we will examine the evolutionary logic of parental investment in a hierarchical fashion, starting from broad individual differences in life history

strategies and ending up with the regulation of genetic expression. We begin by presenting the basics of life history theory and by reviewing its main implications for individual and social differences in parent–child relationships. We then examine how parents modulate investment depending on children’s characteristics, such as sex, age, and physical similarity to their father. Next, we look at the family as a cooperation network in which children reciprocate by providing help to parents, but where there are also opportunities for exploitation, and we discuss cross-cultural variation in the role of children within the family. Finally, we introduce one of the most fascinating topics in the biology of parent–child relations, genomic imprinting and the conflict between paternal and maternal genes *within* the child’s genome.

A Life History Perspective on Parent–Child Relationships

Life History Theory

Life history theory is a branch of evolutionary biology dealing with the strategies that organisms use to allocate their limited time and energy to the various activities that comprise their lifecycle (see Hill, 1993; Kaplan & Gangestad, 2005; McNamara & Houston, 1996; Penke, 2010). All organisms live in a world of limited resources; the energy that can be extracted from the environment in a given amount of time, for example, is intrinsically limited. Time itself is also a limited good; the time spent by an organism looking for mates cannot be used to search for food or care for already-born offspring. Since all these activities contribute to an organism’s evolutionary fitness, devoting time and energy to one will typically involve both benefits and costs; and natural selection strongly favors organisms that are able to adopt an optimal scheduling of activities—with optimal being defined as that which maximizes the individual’s inclusive fitness.

Life history theory employs formal modeling to solve the complex optimization problem of how—and when—to allocate limited resources to gain the maximum reproductive success. Life history strategies (LHS) are, in a nutshell, adaptive solutions to a number of simultaneous fitness trade-offs. Use of the term “strategy” does not, however, imply conscious planning or deliberation or even awareness. The most basic trade-offs are between *somatic effort* (i.e., growth, body maintenance, and learning) and *reproductive effort*; and, within reproductive effort, between *mating* (i.e., finding and attracting mates, conceiving offspring) and *parenting* (i.e., investing

resources in already conceived offspring). From another perspective, the crucial decisions involved in an LHS can be summarized by the trade-offs between *current* and *future reproduction*, and between *quality* and *quantity of offspring* (see Belsky, Steinberg, & Draper, 1991; Ellis, Figueredo, Brumbach, & Schlomer, 2009). Is the organism going to reproduce as soon as it can, or to wait longer, in order to accumulate resources that can then increase offspring “quality” and reproductive success—and thereby the parent’s own inclusive fitness? The more time spent waiting, the more resources (e.g., energy reserves, but also ability and social status) could become available, but the risk of dying before reproducing will increase as well. And, is the organism going to put all of its reproductive effort into increasing the number of offspring, or will it channel resources and parenting effort into increasing the quality and long-term prospects of a few, selected descendants?

One of the most important implications of life history theory is that no strategy can be optimal in every situation; more specifically, the optimal (i.e., fitness-maximizing) strategy for a given organism depends on its ecology and on a series of factors such as resource availability, mortality, and environmental uncertainty. Indeed, organisms usually embody mechanisms that allow them to fine-tune their life histories according to the environmental cues they encounter during development. Within the same species, different individuals can find themselves in dramatically different environmental conditions, which may call for adjustment in the way that strategic trade-offs are resolved. Some individuals, for example, may face higher mortality, perhaps because of predation or diseases; others may live in a place or time in which food is scarce; others still may face unpredictable and rapidly changing conditions in which anticipating the future is extremely difficult. Due to such environmental variability, life history traits and strategies tend not to be genetically fixed, but rather evolve to show adaptive *developmental plasticity* (for an example, see Belsky et al., 1991; Ellis, Jackson, & Boyce, 2006; for a comprehensive account, see West-Eberhard, 2003). Organisms assess their local environments and adjust their strategic allocation choices, following evolved rules that maximize expected fitness in different ecological conditions.

A crucial factor affecting LHS is the pattern of extrinsic mortality; that is, mortality that cannot be prevented by altering the organism’s behavior. More generally, all (totally or partially) uncontrollable

factors that negatively affect reproductive success can be considered sources of *extrinsic mortality-morbidity* (Ellis et al., 2009). When mortality-morbidity is high (e.g., because of virulent diseases, risk of predation, or high levels of aggressive competition), it is adaptive to favor current reproduction by starting mating early, even at a cost for one’s future reproductive potential. Moreover, high extrinsic mortality means that investing in parental care has quickly diminishing returns: As (by definition) parental effort cannot decrease extrinsic mortality-morbidity, offspring’s fitness will not respond to parental care beyond a certain amount. Thus, environmental hazard favors quantity versus quality of offspring and current versus future reproduction, and selects for life histories that invest in mating at the expense of parenting. The same is expected from increases in environmental *unpredictability* (see Belsky et al., 1991; Ellis et al., 2009; Pennington & Harpending, 1988). Resource scarcity, in contrast, *in absence of elevated harshness/unpredictability* has the opposite effect, favoring “slow” life histories and high parental investment in a smaller number of offspring. This happens because in resource-scarce but safe and predictable environments, investment by parents can reliably enhance the fitness prospects of progeny and, thereby, parents’ own inclusive fitness.

Although organisms can gather information about their local environment through direct experience, useful cues can also be provided by conspecifics; especially during the early phases of development, one’s parents can be an excellent source of indirect information (Belsky et al., 1991). Parental behavior and parental investment vary according to the local ecology, to the parent’s own LHS, and to offspring characteristics (see below); thus, offspring can use parents as a source of useful cues about the micro- and macroecological conditions they will (probabilistically) face in the future.

LIFE HISTORIES AND THE SEXES

In sexual species, the two sexes predictably differ on life history–related dimensions; they thus can be expected to employ somewhat different strategies in response to the same cues in the environment. In most species, males tend to engage in higher mating effort and lower parental effort than do females (Geary, 2002; Kokko & Jennions, 2008; Trivers, 1972). In addition, males usually undergo stronger sexual selection (i.e., their reproductive success is more variable) and tend to mature more slowly in order to gain the competitive abilities and qualities

needed for successful competition for mates. Sexual asymmetries in life history strategies can be attenuated in species with monogamous mating systems, and when both parents contribute to offspring care. Compared with other mammals, humans show an unusual degree of paternal investment, and are clearly adapted for the *possibility* of monogamous, long-term relationships (see Chapter 2, by Flinn). However, human paternal care is highly variable and facultative (e.g., Geary, 2005; Quinlan, 2008), and strict monogamy is rarely found, if ever (Marlowe, 2000, 2003).

As a result of basic biological differences, the various components of LHS do not carry the same weight for men and women. The current versus future reproduction trade-off is somewhat more pressing for women: Women's reproductive rate is limited by the long duration of gestation and the conspicuous energetic investment of pregnancy and lactation, and their window for successful reproduction necessarily ends with menopause. In contrast, men can potentially sire many offspring in a very short time, as well as for a more extensive period of their lives. Men's crucial trade-off is the *mating versus parenting* one: The payoffs of high mating effort are potentially much larger for males, who can benefit directly from having access to a large number of partners; women can have only one child at a time (twin pregnancies aside), and thus benefit relatively less from multiple matings.

Life History Strategies and Parent–Child Relationship

Life history theory is a useful tool for understanding individual and societal differences in parent–child relations. Parents' strategies define their levels of investment in children, whereas children may use parental behavior as a cue to ecological conditions and thus adjust their developing life history strategies accordingly. The behavioral calibration of LHS is expected to work alongside genetic and epigenetic transmission, and genetic differences in plasticity can result in developmental patterns of gene-by-environment (G×E) interactions (Belsky et al., 2009; Belsky & Pluess, 2009).

PARENTS' STRATEGIES

Parental investment is one of the key dimensions of LHS. Harsh and unpredictable environmental conditions should reduce parental investment, and men should switch to a reduced investment strategy more readily than women when faced with equivalently harsh and unpredictable conditions. Based on

cross-cultural evidence, Quinlan (2007) showed that levels of paternal care decline steadily with increasing risk of disease (pathogen stress), whereas maternal care decreases at high levels of pathogen stress but *increases* at moderate levels (possibly to compensate for reduced contribution by fathers). In contrast, severity of famine and warfare is associated with reduced maternal care, but only weakly related to paternal care. Another cross-cultural study by Schmitt and colleagues (2003) found that dismissiveness in romantic attachment (associated with low couple stability and low parental investment) increases with increasing mortality rates, fertility rates, and disease risk. Interestingly, the association was stronger in women; men are more dismissing than women at low and moderate levels of environmental stress, but sex differences shrink as environments become harsher.

As indicated above, the crucial LH trade-off for men is that between mating and parenting effort. Indeed, mating opportunity affect men's LHS more strongly than women's. A survey of four hunter-gatherer societies by Blurton Jones and colleagues (2000) showed that the availability of potential new partners for men (indexed by a low sex ratio, i.e., a low proportion of men relative to fertile women) was the strongest negative predictor of marital stability. Marital stability, in turn, is a major determinant of continued paternal investment across cultures. When sex ratios are low, young men tend not to marry, although they are able to marry more easily when they become older (Kruger & Schlemmer, 2009a, 2009b); at the same time, low sex ratios predict higher sexual promiscuity in both sexes (Schmitt, 2005). The local mating system is another key variable. Polygyny often correlates with reduced paternal investment (Marlowe, 2000, 2003), and the relationship between disease risk and reduced paternal investment reported by Quinlan (2007) appears to be mediated—at least in part—by increased polygyny. Another ecological determinant of couple stability is the degree of complementarity between men's and women's contribution to subsistence. In societies in which the sexes contribute resources in approximately equal parts, couple relationships are more stable than in societies in which one of the sexes provides most or all resources (Quinlan, 2008). At the individual level, the allocation of resources to mating versus parenting also depends on age: In men, there is a widely observed tendency to invest preferentially in mating during the first phase of reproductive life, then switch to increased paternal investment (e.g., Kruger & Schlemmer,

2009a, 2009b; Winking, Kaplan, Gurven, & Rucas, 2007).

In summary, life history theory explains how a number of ecological and social factors modulate parental investment and, in turn, affect the quality of parent–child relationships. Romantic attachment is likely a major component of parents' life history strategies (Belsky, 1997a; Chisholm, 1996; Del Giudice, 2009), as romantic attachment styles influence couple stability, fidelity, and long-term commitment, all conducive to parental investment and affectionate parent–child relations. In harsh and unpredictable environmental conditions, parenting becomes harsh, too; parents tend to be less involved, less affectionate, and more prone to neglect their children. Compared with paternal care, however, maternal care is somewhat more resistant to the undermining effects of harsh environments. Fathers' investment in their children is much more variable and heavily influenced by the availability of potential partners, especially when men are relatively young. Low sex ratios are a risk factor for familial instability and father absence (Messner & Sampson, 1990); social factors that lower the sex ratio (e.g., male incarceration, war) or otherwise reduce the number of men who have the resources to be potentially attractive husbands (e.g., unemployment) tend to switch LHS away from parenting and toward short-term mating.

Note that, as a rule, a given population or society will show internal variation in life history–relevant factors; for example local sex ratios may differ widely between cities (or, in large cities, between different neighborhoods), and different subgroups may experience different levels of violence and disease. The possession of adequate resources (e.g., at the family level) may also buffer adverse macroenvironmental effects to some degree—by, for example, reducing the unpredictability of the future (both actual and perceived). In general, it should be kept in mind that an individual's "environment" is a nested hierarchy of ecologies (Bronfenbrenner, 1979), from the macroecological level (e.g., population mortality rates, disease epidemics) to the microecological level (e.g., one's family conditions, but also one's specific place in that family). Individual differences in LHS also depend on genetic differences. All the life history–related traits investigated so far, from sexual maturation timing to romantic attachment, show at least moderate heritability (e.g., Brussoni, Lang, Livesley, & Macbeth, 2000; Figueredo et al., 2004; Mendle et al., 2006, 2009; Rowe, 2000). Moreover, an individual's genetic make-up influences

his or her responsivity to environmental factors (Belsky et al., 2009; Belsky & Pluess, 2009), so that not all people are equally sensitive to the factors we have examined here (see below).

CHILDREN'S STRATEGIES

In the preceding section, we discuss how parental investment and caregiving behavior are affected by ecological factors. In turn, children can use their parents' behavior as sources of information about their own present and future environment. Belsky and colleagues (1991) proposed that attachment security in the first 5–7 years of life acts as a summary of the safety and quality of the child's environment, channeling the child's developmental trajectory along alternative developmental pathways. Attachment is closely linked to the stress response system and regulates the child's feelings of distress, pain, fear, and loneliness; and although attachment security can change during the individual's lifetime, it shows a prototype-like dynamics in which early security/insecurity (established in the first years of life) can continue to affect behavior and development later in life, including adulthood (Fraley, 2002). Secure attachment would lead to later sexual maturation, later reproduction, high parental investment, and a trusting, cooperative interpersonal style; in contrast, insecure attachment would lead to earlier maturation and reproduction, higher mating effort, and an opportunistic, selfish interpersonal orientation. Again, both macro- and microecological factors influence the quality of parent–child relations and children's attachment styles; indeed, the latter instantiate the former, thereby providing guidance to the child.

Even within the same family, parents may invest little in a given child because of a number of reasons, including parents' mental illness, low phenotypic quality of the child (e.g., disabilities, chronic health problems), or the presence of stepparents (Chapter 7, by Anderson). Here, we discuss how the child's sex, age, and birth order can be powerful determinants of parental investment. Parental behaviors are informative because they correlate with macroecological factors (Belsky, 1984; McLoyd, 1990), but also because investment received in the present is an indicator of the investment that the child can expect to receive in the future (Ellis, 2004).

The original evolutionary model of socialization advanced by Belsky and colleagues has been integrated and revised over the years (e.g., Belsky, 1997a; Chisholm, 1993, 1996, 1999; Del Giudice, 2009;

Simpson & Belsky, 2008) and has received extensive empirical support. For example, recent genetically informed studies have confirmed the predicted relationship between stressful, negative parent–child relationships and earlier puberty timing in girls (Belsky et al., 2007; Ellis & Essex, 2007; Tither & Ellis, 2008). More recently, data show that attachment security in infancy, known to be causally influenced by quality of parental care, itself predicts pubertal maturation; just as predicted, early insecurity forecasts earlier onset and completion of pubertal development, as well as earlier age of menarche (Belsky, Houts, & Fearon, 2010).

Subsequent elaborations of the model have emphasized that early strategic calibration may be revised at later developmental stages; LHS are not set in stone during early childhood and thus can respond to changes in the environment and to the new information provided by social interaction with peers (see Del Giudice & Belsky, 2010). Evolutionary theory and cross-cultural evidence also indicate that maternal and paternal investment respond in different ways to the same ecological factors (see above); thus, attachment relationships with the two parents may carry distinct types of information, conceivably influencing child development in different ways. Although some evidence suggests that insecure attachment to the mother and to the father predict different developmental outcomes (reviewed in Del Giudice, 2009), the data are still too sketchy to draw reliable conclusions. Unfortunately, the very research that now shows that early insecurity in the infant–mother relationship forecasts earlier pubertal maturation lacks measurement of infant–father attachment security.

Because of parent–offspring conflict about investment, children do not simply accept whatever parents do with them; rather, they actively try to maximize parental investment and commitment. In this vein, Chisholm (1996) proposed that children's insecure attachment styles are adaptive strategies designed to respond to different “safety threats.” In the case of parents who are willing, but *unable* to consistently invest in offspring—for example because of scarce resources or competing demands on parents' time—the insecure-ambivalent strategy maximizes the available investment by increasing signaling of need, immature behavior, and emotional dependence. When parents are *unwilling* to invest, however, the insecure-avoidant strategy is favored; emotional distancing and self-reliance reduce the demands on parents, thus protecting the child from being abandoned or abused while

still vulnerable. From this perspective, attachment styles are not the passive result of the child's experience with parents, but rather the outcome of an active negotiation process based on investment dynamics.

INDIVIDUAL DIFFERENCES IN PLASTICITY

A central premise of much developmental psychology focused on the family is that early experiences influence the child's future psychological and behavioral development. As a result, not only is there extensive research on how mothers, fathers, siblings, peers, child care, schooling, and even neighborhoods shape children's functioning over the short and long term, but also on the psychological, physiological, and neurological mechanisms that mediate such effects of experience on development. What is rarely considered, however, and yet is central to an evolutionary analysis of development, is why natural selection should even craft an organism whose future development is shaped by childhood experiences.

The minute one appreciates that the future always has been uncertain and will always, presumably, remain that way, there are grounds for questioning the assumption that experience shapes development. Would not this only make biological sense if contexts of development, broadly conceived, proved tolerably stable within a generation and perhaps across adjacent ones? Otherwise, how could setting one's developmental sail on the basis of the winds encountered early in life achieve a destination later in life? Unstable environments would blow the ship of development off course.

Such reasoning led Belsky (1997b,c, 2005) to hypothesize that children should vary in their susceptibility to rearing, with some being more susceptible to parenting and other experiential influences in and outside of the family and some being less susceptible. By bearing such diverse children, parents would end up hedging their bets on an uncertain future. If things turned out as consciously or unconsciously expected—both within and across generations—then a child whose development was guided by parentally shaped earlier experience should flourish; but if it did not, then it could be the child who proved less responsive to such developmental experiences who would realize a fitness advantage. Variation in susceptibility would benefit both parents and siblings, whose inclusive fitness would be increased through their relatedness to the “successful” offspring (the relatedness coefficient between siblings and between parent and offspring

is 0.5, where 1.0 indicates a complete overlap of genetic interests).¹

Boyce and Ellis (2005) have come to a similar conclusion, that children should vary in their susceptibility to rearing influences, but for different evolutionary reasons. On the basis of conditional adaptation logic, they hypothesize that those growing up in especially good conditions should be especially responsive to the environment, as this would enable them to take advantage, indeed embody, many of these resources, making them more competitive in the world in which they would eventually function. At the same time, those growing up under harsh conditions should prove highly susceptible, too, as this would promote antagonism and vigilance, making them more likely to survive and cope in the hostile world that they have been prepared to encounter. All others, according to this analysis, should prove to be more “fixed” than “plastic” strategists, to borrow Belsky’s (2000, 2005) terminology.

As it turns out, evidence increasingly indicates that some individuals appear more susceptible than others to environmental influences—“for better *and* for worse,” meaning that they are more likely than others to both benefit from supportive conditions *and* be adversely affected by negative conditions (Belsky, Bakermans-Kranenburg, & van IJzendoorn, 2007). Indeed, evidence indicates that this may be true of highly negatively emotional infants and toddlers, highly physiological reactive individuals, and those carrying certain genes (Belsky & Pluess, 2009; Orbadovic & Boyce, 2009). In fact, after carefully scrutinizing recent research on G×E interactions in predicting behavioral development, Belsky and associates (2009; Belsky & Pluess, 2009) have concluded that multiple alleles regarded by many psychiatric geneticists as “vulnerability genes” because they apparently increase the likelihood of psychiatric disorder in the face of stress may actually be better referred to as “plasticity genes” (Belsky et al., 2009; Belsky & Pluess, 2009). And this is because

those carrying these genes not only function more poorly than all others under adverse circumstances, but function better than all others under benign and supportive conditions. The existence of plasticity genes and the resulting G×E interactions help to explain why, in behavior genetic studies, “shared” environmental effects (those which make siblings in the same family more alike) are consistently found to be small compared to “nonshared” ones. Individual differences in susceptibility also contextualize the claim, based on the findings of behavior genetics, that parental behavior has no lasting effects on children’s development (e.g., Harris, 1998; Pinker, 2002). Whether parents’ behavior affect a child’s development seems to depend, in large part, on the child itself and his or her genetic make-up.

Children’s Characteristics and the Modulation of Parental Investment

Morally upsetting as it may appear, evolution does not favor indiscriminate parental investment—or unconditional love—regardless of offspring’s characteristics (Daly & Wilson, 1988). Limited resources must be allocated wisely, and parents embody evolved decision mechanisms designed to channel investment toward those offspring who offer the best chances of high fitness returns. In humans, parental discrimination may become manifest in the parent’s feelings; for example, some children may elicit more affection and caring than others, even if the actual decision mechanisms work partially or completely outside the parent’s awareness. Parental discrimination inevitably becomes more intense when resources are especially scarce; an extreme, dramatic example of parental discrimination is infanticide, which is especially frequent in harsh ecologies (see Hrdy, 1999). Even in more benign environments, not all children are necessarily equal in the eyes of their parents, and the consequences for children may be very real—for better or for worse. In this section, we explore three characteristics of children—sex, age, and physical resemblance to the father—that have been shown to affect parental investment across cultures.

Sex-biased Investment

Preferences for sons or daughters are extremely common in human families, yet very complex to predict and analyze. Parents can benefit from investing preferentially in children of one sex for a number of different reasons, and patterns of sex-biased investment depend in subtle ways on personal and ecological variables (Sieff, 1990). The underlying

¹ By a simplified account, the relatedness coefficient r can be defined as the probability that two individuals share the same allele at any given locus by (recent) common descent. As a probability, r ranges between 0 and 1. For example, in diploid species the parent–offspring relatedness is $r = 0.5$, since (with Mendelian transmission) an allele present in one of the parents has a 50% probability of ending up in any given offspring. Relatedness can be defined more generally (and rigorously) as the genetic similarity between two individuals, A and B, relative to the average genetic difference between A and a randomly chosen member of the population. Thus, r can be treated as a regression coefficient and can take negative values (see Grafen, 1985).

logic is that parents should prefer to invest in the sex with the best expected fitness returns. In turn, the fitness returns of a child depend on many ecological and cultural factors. For example, if daughters provide more help to their parents by caring for younger siblings, they may “repay” their investment costs more than sons; securing bridewealth is another way daughters in which may contribute to the welfare of parents and siblings. On the other hand, in some contexts, it is sons who provide more help than daughters—by, for example, providing food or economic resources and staying with the family for a longer time (e.g., because daughters marry young and then live with the husband’s family). This kind of effect (known in the literature as *local resource enhancement*) has been used to explain the patterns of daughter favoritism in breastfeeding observed in Dominica (Quinlan, Quinlan, & Flinn, 2005) and in North American Hutterites (Margulis, Altmann, & Ober 1993).

Another important perspective on sex-biased parental investment is provided by the Trivers-Willard hypothesis (TWH; Trivers & Willard, 1973). The TWH stipulates that, when one sex benefits from high investment more than the other, parents in good conditions (i.e., with lots of resources to invest) should invest preferentially in that sex, whereas parents in poor conditions should invest in the other. Because males usually have higher reproductive variance than females, they benefit relatively more than females from good conditions; this is due to the fact that males in good conditions can out-compete other males. Moreover, in stratified societies, women can marry into higher classes more easily than men, and generally face less competition for mates than do low-status men; thus, parents of low social status may improve their inclusive fitness by investing in daughters, whereas high-status parents do so by investing preferentially in sons. Parents can fulfill the TWH in three independent ways: (1) by biasing the sex ratio at birth, so that mothers in poorer conditions give birth to more daughters; this can be accomplished by physiological mechanisms that respond to stress, nutritional level, and so on; (2) by selective infanticide or abandonment of neonates of one sex; and (3) by differential investment in nutrition, health, education, and in general by sex-biased distribution of family wealth.

The effect of maternal conditions (i.e., nutrition, education, socioeconomic status) on the sex ratio at birth has received some support from demographic studies in modern societies (Almond & Edlund, 2007; Chacon Puignau & Jaffe, 1996; Gibson &

Mace, 2003; Mathews, Johnson, & Neil, 2008; see also Cameron & Dalerum, 2009). In some of this work, maternal conditions also predict sex biases in infant mortality (Almond & Edlund, 2007; Chacon et al., 1996; Volland, Dunbar, Engel, & Stephan, 1997), suggesting differential investment in already-born infants. However, effects tend to be rather small, and other investigations have failed to find evidence in favor of the TWH (e.g., Guggenheim, Davis, & Figueredo, 2007; Stein, Zybert, & Lumey, 2004). The TWH also provides an explanation of the fact that female infanticide has been historically more frequent in upper social strata, such as Indian high castes (Dickemann, 1979). However, it has been considerably more difficult to find consistent support for Trivers-Willard effects when measuring parental investment indicators like breastfeeding, investment in children’s education and health, and so on. The strongest evidence in favor of the TWH comes from research on small-scale societies such as the Kipsigi and Mukogodo in Kenya, the Arsi Oromo in Ethiopia, the Yomut in Iran, and Hungarian Gypsies (Berezkei & Dunbar, 1997; Borgerhoff Mulder, 1998; Cronk, 1989, 1991a,b; Irons, 2000). Cronk (2007) discusses the many theoretical and methodological difficulties involved in properly testing the TWH in large-scale industrialized societies.

An important insight emerging from evolutionary research on sex-biased investment is that parents are often unaware of their actual favoritism patterns. Marked patterns of daughter-biased investment, for example, have been found in populations in which parents express strong and culturally shared preferences for sons (Cronk, 1991a; Gibson, 2008; Pennington & Harpending, 1993). This, of course, adds to the difficulty of studying parental investment through self-report data. Finally, parents do not always agree in their preferences for sons versus daughters. Studies in various societies have found that fathers tend to invest more in sons, and mothers tend to invest more in daughters, although there are exceptions (reviewed in Gibson, 2008; Godoy et al., 2006). Godoy and colleagues (2006) proposed to explain this effect with an extension of the TWH, whereby the parent facing less resource constraints (usually the father) maximizes his (or her) fitness returns by investing in sons.

Age-related Preferences and Birth Order

In humans, mortality is highest around birth and decreases through childhood, with an all-time minimum in middle and late childhood, whereas fertility

peaks in late adolescence and early adulthood. A child's *reproductive value* at a given age is his or her expected number of future offspring, and is a function of expected survival and expected reproduction; reproductive value is lowest at birth and rises steadily until early adulthood, then declines (see Sear, in press). When faced with difficult allocation decisions, parents should choose—all else being equal—to invest more in older children, whose reproductive value is highest. Preferences for older children are widespread and may have dramatic implications. Research on infanticide shows that younger children are consistently at higher risk of being killed by parents (e.g., Daly & Wilson, 1984; Hill & Hurtado, 1996). When Meryl Streep was required to give up one of her children for extermination in the film *Sophie's Choice*, about the legacy of the world War II, chances are that she would have chosen to save her older child and surrender her younger one to the Nazi murderers, had she been the real mother of a real child confronting this horrendous situation.

Firstborns are also favored when resource transfer from parents is concerned; cross-culturally, primogeniture is by far the most common pattern of inheritance. The advantages of firstborns can be counterbalanced by the fact that, as parents age, they face fewer competing demands for investment allocation (mating effort and investment in future offspring). Thus, laterborns can also end up getting a relatively large share of investment from parents, with middleborns receiving the least (see Salmon & Daly, 1998). Finally, the effects of age often interact with those of sex; for example, in societies in which sons are favored, children with many older brothers may be at special disadvantage (for extended discussion see Sear, in press).

Father–Child Resemblance

Genetic relatedness between a man and his putative children, including uncertainty about that relatedness (i.e., paternity uncertainty), is one of the crucial factors determining how much the man is expected to invest (see Chapter 11, by Goetz and Romero). Investing one's resources in a genetically unrelated child entails large fitness costs; thus, natural selection can be expected to favor discrimination and selective investment by fathers. Because females can gain material, social, and genetic benefits from extra-pair mating, cuckoldry is a real risk in most paternally investing species. To mitigate this risk, natural selection has favored psychological and behavioral mechanisms in males that function to increase paternity certainty and limit investment in

unrelated offspring (e.g., Møller & Birkhead, 1993; Whittingham, Taylor, & Robertson, 1992).

One way for fathers to assess the likelihood that a child is their biological offspring is to rely on phenotypic similarity. Given the heritability of most physical traits, the more a child resembles his or her putative father, the greater the father's paternity confidence is likely to be. Greater perceived similarity, therefore, should translate into greater investment. Based on this logic, several empirical studies have tested—and confirmed—the impact of father–child similarity on paternal investment. Perceived facial resemblance in children positively predicts fathers' emotional closeness and investment (time spent with the child, involvement in the child's education; Alvergne, Faurie, & Raymond, 2010; Apicella & Marlowe, 2004, 2007; Li & Chang, 2007). There seems to be a good match between actual similarity (as rated by external judges) and fathers' perceived similarity (Alvergne et al., 2010).

The impact of similarity on paternal investment is even stronger when the father and the mother are separated; that is, when the father has no extra reasons to engage in parental care—for example, maintaining a good relationship with the mother or displaying one's good qualities as a partner (Apicella & Marlowe, 2004, 2007). Burch and Gallup (2000) found an association between perceived resemblance and the self-reported quality of father–child relationships in a sample of men who had committed domestic violence. Interestingly, phenotypic similarity seemed to affect the quality of paternal care only with respect to (possibly) biologically related children; when the child was *known* to be biologically unrelated, father–child resemblance had no significant effect.

Facial resemblance is not the only cue of phenotypic similarity available to fathers. Olfactory similarity also predicts paternal investment (Alvergne, Faurie, & Raymond, 2009), and fathers are more affectionate and attentive toward the children they can recognize by their smell (Dubas, Heijkoop, & van Aken, 2009). Some effects of olfactory recognition have been reported in mothers, too; mothers punish less frequently those children whose smell they can recognize (Dubas et al., 2009).

While discussing parent–child resemblance, it should be noted that infants and children do not, on average, resemble their parents very closely. Correct recognition rates are above chance but still far from perfect. Taken together, the empirical data suggest that children resemble both the mother and the father, with an overall tendency for newborns

and infants to resemble their *mother* more than their father (see Alvergne, Faurie, & Raymond, 2007; Bressan & Grassi, 2004). In the study by Alvergne and colleagues (2007), male (but not female) children started to resemble their father more than their mother at about 2–3 years of age, an intriguing finding still in need of replication and (if confirmed) explanation.

Despite the weak resemblance between fathers and infants at birth, mothers and other maternal relatives are especially prone to attribute paternal resemblance to their newborns. This can be interpreted as a way to manipulate fathers' perception of similarity, thus increasing paternal commitment and investment (Alvergne et al., 2007; Bressan, 2002; Daly & Wilson, 1982). So far, there have been no investigations of how children who do not resemble their father react psychologically. An evolutionary-informed perspective suggests that the lack of similarity may be a specific source of distress, and that children (like their mothers) should actively manipulate their father's perception of similarity so as to maximize their commitment and parental investment.

Given that fathers are so sensitive to phenotypic similarity, should it not be the case that children evolve to resemble their biological fathers as closely as possible? The answer to this question turns out to be far from obvious. On the one hand, children benefit from advertising their identity to their putative father when he actually is the biological father; on the other, however, they also benefit from concealing their identity when the putative father is *not* the biological one. The mathematical models developed so far give contrasting results, with some models predicting increased selection for resemblance with increased paternity uncertainty (Johnstone, 1997) and others predicting the opposite effect (Bressan, 2002; Pagel, 1997). In any event, these models converge on the prediction that enhanced father–child resemblance should not evolve easily (if it can evolve at all). The benefits of concealing one's identity may account for the relatively low degree of resemblance between human infants and their fathers. Note in this regard that it might not just be nonbiological offspring who benefit from relative infant anonymity, but the cuckolding female partner as well.

Children As Providers: Caring, Helping and Exploitation

As in other animal families, the primary role of children is that of receiving investment from parents.

At the same time, however, human children actively contribute to the family system as resource providers and caregivers. The anthropological literature clearly shows that daughters play a crucial role as helpers and alloparents (i.e., individuals who provide care without being the young's parents; see Hrdy, 2005). In traditional societies, women who can count on the help of daughters have higher reproductive success than do women who only have sons or young children (e.g., Flinn, 1989; Turke, 1988). Several studies show that the presence of older siblings improves child survival (Sear & Mace, 2008).

Whereas daughters often provide care to younger siblings, they can also contribute to the household economy by helping in domestic work. In traditional societies, children of both sexes spend considerable time foraging; in safe, resource-rich ecologies they may contribute substantially to their own caloric intake (see Kramer, 2005). For example, Maya children produce about 50% of what they consume by the age of 6 or 7 years (Kramer, 2002). Even though children are less efficient foragers than adults, they can devote more time to foraging because they have fewer competing activities to carry out, and the costs of helping can be relatively low compared to their fitness benefits.

The onset of juvenility, or *juvenile transition* (Del Giudice, Angeleri, & Manera, 2009), seems to be a crucial turning point in children's helping behavior. Juvenility is the biological label for middle childhood (from about 6–7 to 10–11 years of age in modern societies); it is a period of intense social learning and dramatic cognitive development, marked by specific hormonal and neurobiological changes and by the intensification of behavioral sex differences (Campbell, 2006; Del Giudice et al., 2009). For example, in the Maya population studied by Kramer (2005), juveniles play a substantial role as resource providers during the second phase of marriages (from about 10 to 20 years of marriage), when parents must support many children still living at home.

More generally, Lancy and Grove (in press) argued, based on cross-cultural evidence, that juvenility is the time when children start “getting noticed” by adults. For the first time, juveniles are assigned tasks involving expectations of responsibility. Indeed, in many societies young children are more or less ignored by adults, but as juveniles, they start to become involved in duties and chores and to assume a recognized social identity. Children help in a wide range of tasks, including gardening,

herding, hunting, weaving, ceramics, and canoe-making; girls seem to undergo this transition from play to work earlier than boys (see Lancy and Grove, in press).

The importance of children's help should not lead us to ignore the fact that, because the relatedness between parents and children is only partial, the interests of parents and children do not fully coincide; in fact, at times they may clash with one another. Children's helping can take any shape from harmonious cooperation to parasitic exploitation by parents. The line is especially fine in impoverished Third World societies, in which child labor is a common and growing phenomenon. As extensively documented by Lancy (2008, ch. 10), in many countries, children are forced to begin earning their keep at younger and younger ages; the dismantling of traditional institutions and extended kin networks takes children out of the village and into the city, where the traditional, slow transition to adult work is dramatically accelerated. Moreover, the loss of social control on parents by kin members and neighbors means that child abuse can go unchecked.

Parents in harsh and unpredictable ecological conditions react by lowering their investment in children, leading to typical high mortality/high fertility patterns and unconcerned, neglectful, or abusive parenting. Parents may come to see children as a resource to exploit, in a paradoxical game in which children provide for their parents (sometimes they may be the family's primary income earners), and the border between cooperation and exploitation becomes blurred. It has been argued that, in some cases, street children may be better off by themselves (or with their siblings as caretakers) than at home with their abusive parents (e.g., Aptekar, 1992). These social and economic processes depend on a number of psychological mechanisms that are products of our evolutionary history: facultative parental investment, the modulation of LHS in response to environmental stress, and the willingness of children (especially juveniles) to help their parents and to actively engage in chores that contribute to their family's welfare.

Modern Childhood: Overprotection or Adaptive Strategy?

Anthropologists who study childhood in traditional societies are struck by the contrast between the traditional view of childhood and the modern ideal that is prevalent in the West and in East Asia. The modern ideal sees childhood as taking place in the context of a nuclear, egalitarian family in which parents share

their caretaking responsibilities and unconditionally love and invest in their offspring. Every child is inherently worthy and has a right to life and happiness; the well-being of children is the primary concern of their parents, who instruct them and care for them well into adolescence. This ideal pattern is complemented by high investment in intellectual stimulation right from birth (or even before), supervised learning, formal schooling, an extended period of play and immaturity, and a protracted adolescence.

The traditional view of children is strikingly different from the modern one: children are regarded as the lowest-ranking members of the society, grow up in extended families, and are cared for by a network of individuals which includes older siblings and grandmothers (but with fathers rarely involved in direct caretaking). Selective infanticide and abandonment are relatively common, especially for children of the wrong sex or with developmental defects, making it clear that offspring are expendable. Children are largely ignored by adults and considered somewhat uninteresting as individuals, at least until they reach juvenility; they are then expected to return some of their parents' investment in the form of helping (Lancy, 2008). Of course, this does not mean that parent-child relations in traditional societies are unloving or careless, although they may appear as such to the eye of a modern Western parent (or developmental psychologist).

In the tension between these views (and between the corresponding cultural practices), modern childhood stands out as absurdly overprotected, excessively long, and even "out of touch" with our evolved dispositions. Lancy (2008) notes that "our society is a neontocracy where kids rule" (p. 373), in contrast with the gerontocratic organization of traditional cultures. This, however, may be a premature conclusion: In fact, the Western pattern of hyperinvestment in children could reflect an adaptive strategy responding to recent dramatic changes in social and ecological conditions. Modern industrialized societies have extremely low mortality rates (especially in the first years of life), and the most common sources of extrinsic mortality/morbidity (diseases, warfare, predation) are greatly reduced compared with their premodern levels. This alone should push LHS toward high levels of parental investment.

In parallel, social competition increases and technology becomes more sophisticated. Both high-level jobs and daily living require unprecedented amounts of cognitive flexibility and information manipulation (Gottfredson, 2007). As a result, children become more costly, and the main currency of

parental investment becomes education. Because of reduced environmental harshness and increased need for high-quality cognitive skills, the threshold of diminishing returns for parental investment is shifted upward. The predicted outcome is a reduction in fertility and a corresponding increase in the amount of parental investment expended on each child (e.g., Kaplan, 1996; Kaplan & Lancaster, 2000; Shenk, 2009). This facultative plastic response of life history-related psychological mechanisms may capitalize on recent genetic selection for increased biparental care and higher cognitive flexibility, driven by the social and environmental changes brought about by agriculture (Cochran & Harpending, 2009).

In summary, modern childhood may turn out to be—at least in part—an adaptive response to modern environments. From an evolutionary standpoint, idealizing traditional childrearing could be just as myopic as taking for granted the romantic worldview criticized earlier. Children in traditional societies learn casually and mostly by observation rather than through formal schooling; but then, they only need to master a fraction of the knowledge required for successful living in a stratified and technologically advanced society. Likewise, intellectual stimulation from infancy and an extended phase of play and exploration may be advantageous in a competitive and fast-changing society where creativity, flexibility, and innovation are highly rewarded.

The Family Within: Imprinted Genes and Parent–Child Conflict

So far, we have discussed how investment dynamics are played out by individuals whose genetic interests are partly conflicting. Evolutionary genetics, however, shows that conflicts of interest run much deeper than that: In fact, conflicts about parental investment can arise not only between parents and children, but also between different genes *within the child*—specifically, between genes inherited from the mother and genes inherited from the father. This form of intragenomic conflict derives from the special characteristics of imprinted genes, and its evolutionary implications are spelled out in the *kinship theory* of genomic imprinting (Haig, 1997, 2004; Wilkins & Haig, 2003).

The Kinship Theory of Imprinting

A gene is said to be *imprinted* if its expression depends on its parent of origin (i.e., on whether it was contained in an ovum or a sperm). For example,

IGF2 (a gene coding for an important growth factor) is paternally expressed in humans, and its homologues are paternally expressed in various mammals including rats, mice, and sheep. This means that although every individual inherits two copies of the gene (one from each parent), only the paternally derived copy is actually expressed, whereas the maternally derived one is silenced and has no effect on the organism's development. Gene silencing is accomplished through reversible epigenetic mechanisms; complex imprinting patterns can be observed as, for example, some genes show parent-specific expression only in specific cell types or only during certain phases of development. To date, imprinted genes have only been found in mammals and angiosperm plants; according to current estimates, less than 1% of the mammalian genome is imprinted (Wilkins, 2008).

Let us consider parent–offspring conflict from the perspective of imprinted genes. A maternally derived allele in the offspring has a 50% probability of ending up in a future sibling. But if there is any degree of multiple paternity, this probability will be lower than 50% (possibly much lower). In other words, the relatedness between siblings is *asymmetric* when one looks at the maternal and paternal halves of the genome. For imprinted genes, this phenomenon has remarkable implications: Because a paternally expressed gene is always less strongly related to future siblings than its maternally expressed counterparts, it can be expected to function in a way that discounts the well-being of future siblings to the benefit of the individual offspring in which it resides. Thus, paternally expressed genes are expected to “side” with the offspring in the (up) regulation of maternal investment, and to evolve so as to increase the transfer of maternal resources to the offspring—for example, by increasing the rate of fetal growth. Maternally expressed genes are expected to evolve in the opposite direction, thus inhibiting the transfer of maternal resources to the offspring (so as to conserve resources for future offspring or those already born). The intensity of conflict between maternally and paternally expressed genes is expected to increase with increasing likelihood of multiple paternity, and can be completely avoided only in truly monogamous mating systems (that is, in exceedingly rare conditions).

In summary, the kinship theory of imprinting predicts that paternally expressed genes will evolve as “resource enhancers,” increasing maternal investment toward the individual offspring; they are also expected to increase the demand behavior of

offspring in direct sibling competition. In contrast, maternally expressed genes should become “resource inhibitors” and reduce the individual offspring’s demands in order to favor siblings as a group (Haig & Wilkins, 2000). In species like humans, in which both mothers and fathers provide parental investment, the *generalized kinship theory* developed by Úbeda (2008) predicts that the effects of imprinted genes should *reverse* later in development (typically after weaning), with paternally expressed genes reducing offspring demands and maternally expressed genes increasing them. In other words, paternal genes should increase the offspring’s cost when the mother is investing the most (i.e., during pregnancy and lactation), but reduce the offspring’s cost as soon as the father’s own contribution increases. Crucially, such reversal is expected even if the father always contributes less than the mother—all it takes is a *relative* increase in paternal investment over the course of development.

The Role of Imprinted Genes in Human Development

Many imprinted genes are involved in the regulation of fetal growth and affect the level of maternal investment before birth. Examples include the insulin-like growth factor II gene (*IGF2*; paternally expressed); *H19* (maternally expressed), which acts as a suppressor of the action of *IGF2*; and the placental gene *IPL* (also maternally expressed), which prevents placental overgrowth (see Haig, 2004). Many imprinted genes, however, are active after birth, and a substantial proportion are expressed in the brain (Isles, Davies, & Wilkinson, 2006). Thus, imprinted genes may continue to participate in the regulation of investment dynamics by affecting infant and child behavior. Likely targets of genetic action are hunger and food preferences, but several other behaviors can potentially act as resource enhancers/inhibitors—including crying, attention-seeking, emotional dysregulation, dependency, and so on (Brown & Consedine, 2004; Isles et al., 2006). Indirect evidence suggests that imprinted genes are probably involved in the regulation of critical neurotransmitter systems such as dopamine, serotonin, and γ -aminobutyric acid (GABA). Even more intriguingly, there are cues that imprinted genes may exert an impact on the oxytocin and vasopressin systems, which are crucially involved in the neurobiology of parent–child attachment (Davies, Lynn, Relkovic, & Wilkinson, 2008).

At present, most of the empirical evidence for behavioral effects of imprinted genes in human

children comes from the study of two imprinting-related syndromes caused by mutations or deletions on the long arm of chromosome 15, Angelman syndrome (AS) and Prader-Willi syndrome (PWS). These disorders result from opposite patterns of genetic disruption and, as predicted by the kinship theory, show broadly opposite effects on infant investment demands (see Brown & Consedine, 2004; Crespi & Badcock, 2008; Úbeda, 2008). Angelman syndrome, resulting from paternal overexpression and/or maternal underexpression, is associated with increased demands on the mother (e.g., enhanced activity, prolonged suckling, bouts of laughter, and sleeping problems), whereas PWS, resulting from maternal overexpression and/or paternal underexpression, is associated with reduced demands on the mother (e.g., decreased activity, poor suckling, undergrowth, weak crying, and sleepiness). In PWS, hunger regulation changes dramatically after infancy, with PWS-affected children developing insatiable appetites and often becoming obese. An early explanation for this inversion is that the child’s growing appetite for other kinds of food reduces consumption of breast milk, thus lowering the metabolic burden on the mother (Haig & Wharton, 2003). However, the generalized kinship theory (Úbeda, 2008) provides a more elegant explanation, as the reversal of genetic effects observed between infancy and childhood is fully consistent with the pattern predicted by the theory. Overexpression of maternal genes is expected to reduce offspring’s demands during infancy, when the mother’s relative contribution is highest (e.g., poor suckling and undergrowth reduce the cost of lactation), but increase them when the father’s relative contribution becomes more substantial (e.g., weaned children can feed on paternally provided food).

We have just begun to understand the implications of genomic imprinting for the development of children’s behavior and parent–child relations—and so far there has been virtually no application of these ideas to mainstream developmental psychology. Imprinted genes participate in the key neurobiological processes underlying emotional regulation, attachment, and social behavior. Human family life is complex, and parental investment in our species can extend for very long periods of time and even through multiple generations. It is thus reasonable to anticipate that imprinted genes will be found to affect a wide range of processes, including parent–child attachment, adolescent conflict, and the development of psychopathology.

Crespi and Badcock (2008) reviewed a large body of evidence linking imprinted genes to the etiology of autism and psychosis, and proposed that autistic spectrum conditions are associated with a “paternally biased” pattern of brain development (i.e., overexpression of paternal genes and/or underexpression of maternal genes), whereas psychotic spectrum syndromes would be associated with a “maternally biased” development (see Del Giudice et al., 2010, for a sexual selection perspective on the evolution of autism- and psychosis-related personality traits and the associated imprinted patterns). Haig (2010) proposed that imprinted genes could have been conspicuously involved in the evolution of several key features of the human life history, such as early weaning and slow childhood growth (see Chapter 2, by Flinn); finally, a recent model by Úbeda and Gardner (2010) linked imprinted genes to the development of altruism versus selfishness in children.

Conclusion

Long, emotionally intense parent–child relationships are a defining feature of our species and a crucial aspect of our psychology. Adopting the perspective of investment dynamics makes it possible to build a sophisticated general theory of these relationships. The evolutionary framework presented here gives meaning and organization to many psychological phenomena at different levels of analysis—from the impact of macroecological factors on parents’ behavior to the subtleties of genomic imprinting and G×E interactions. As we anticipated, evolutionary-informed predictions are often in good agreement with mainstream developmental psychology—for example, both emphasize the role of harsh environments in determining negative parenting and insecure parent–child relations. The evolutionary approach puts these findings in a broader perspective and adds specificity to the theory, for example by singling out *extrinsic mortality-morbidity* and *unpredictability* as crucial features of the environment—among many possible others—that parents and children use to calibrate their life history strategies. In other instances (e.g., father–child resemblance), evolutionary predictions have some correspondence in folk knowledge, but took an explicitly biological focus to be precisely articulated and tested. Finally, several of the most intriguing phenomena described here simply could not be discovered (or understood) without the benefit of an evolutionary approach. They include the effect of early parent–child relations on puberty timing, the

conflict between maternal and paternal genes in determining infant behavior, and the existence of differential susceptibility to the rearing environment.

Concentrating on individual phenomena, however, is not the best way to appreciate the contribution of evolutionary theory to the understanding of family relations. The real promise of evolutionary psychology lies in its integrative nature: What could be a collection of weakly related phenomena, hypotheses, and mini-theories turns into a well connected and hierarchically structured theoretical edifice. Most importantly for developmental psychologists, inhabiting that edifice does not require one to throw away the empirical yield of decades of research; rather, old insights find new explanations, previous knowledge is transformed and connected in unexpected ways, and new opportunities for discovery are revealed. Careful biological reasoning is also a powerful antidote to idealistic distortions of childhood and parenthood, to which—as experience shows—it is very easy to succumb. The psychology of parent–child relationships can no longer afford to remain disconnected from its biological roots.

Future Directions

One of the most important tasks for the next future will be to explore and clarify the relations between what we have called “investment dynamics” and “affective dynamics.” Attachment theory can be thoroughly redescribed in an evolutionary perspective (e.g., Simpson & Belsky, 2008), thus raising a number of interesting and still unasked questions: What is the relationship between parents’ life history strategies and children’s attachment styles? How do factors such as children’s sex and parent–child resemblance affect the formation and development of emotional bonds? What behaviors on children’s part may be interpreted as attempts to gather reliable information about the local ecology? Which emotional systems are involved in these processes? How do macro- and microecological factors interact to shape attachment security? And so on. Evolutionary psychology may provide excellent theoretical foundations to the study of development, but it will not be embraced until it can be readily connected to the emotional life of parents and children.

Another crucial and under-researched topic is that of the decision-making mechanisms mediating parental investment. Evolutionary models make predictions about parental behavior, but they do not specify the proximate mechanisms that enable

adaptive decision-making. In part, decision processes can be expected to work automatically and outside consciousness; in many cases, however, they may also depend on conscious thought and deliberate reasoning. These two levels may act synergistically, but disconnections are also possible (see, for example, the section on sex-biased investment). In addition to understanding how these mechanisms work, it would be extremely interesting to understand when a given decision-making process should be carried out automatically—and when it should be *designed* so as to remain out of the parent's awareness. The same questions can be asked of decision-making in children; for example, is deliberate reasoning involved in the behavioral manifestations of LHS? Do children possess conscious representations of environmental unpredictability and other life history–relevant parameters, and will changes in these representations feed back on children's behavioral strategies?

Finally, future progress in this area will depend on tighter integration with neurobiology and genetics. Parent–child relations are mediated by intricate neural and hormonal systems, which in turn depend on genetic expression and regulation. Modern genetics is sophisticated enough to deal with individual differences in plasticity, experience-dependent epigenetic regulation, and conflict between maternal and paternal genes. Evolutionary endocrinology (Ellison & Grey, 2009) and evolutionary neuroscience (Platak & Shackelford, 2009) are rapidly advancing fields that can bring invaluable contributions to the study of family relations.

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