

Parent–Offspring Conflict Theory: An Evolutionary Framework for Understanding Conflict Within Human Families

Gabriel L. Schlomer
Arizona Center for Research and Outreach, University of
Arizona

Marco Del Giudice
University of Turin

Bruce J. Ellis
University of Arizona

Decades of research demonstrate that conflict shapes and permeates a broad range of family processes. In the current article, we argue that greater insight, integration of knowledge, and empirical achievement in the study of family conflict can be realized by utilizing a powerful theory from evolutionary biology that is barely known within psychology: parent–offspring conflict theory (POCT). In the current article, we articulate POCT for psychological scientists, extend its scope by connecting it to the broader framework of life history theory, and draw out its implications for understanding conflict within human families. We specifically apply POCT to 2 instances of early mother–offspring interaction (prenatal conflict and weaning conflict); discuss the effects of genetic relatedness on behavioral conflict between parents, children, and their siblings; review the emerging literature on parent–offspring conflict over the choice of mates and spouses; and examine parent–offspring conflict from the perspective of imprinted genes. This review demonstrates the utility of POCT, not only for explaining what is known about conflict within families but also for generating novel hypotheses, suggesting new lines of research, and moving us toward the “big picture” by integrating across biological and psychological domains of knowledge.

Keywords: parent–offspring conflict, life history theory, genomic imprinting, prenatal conflict, sibling relations

Conflict within human families is an important issue that has attracted considerable attention from developmental psychologists. Indeed, decades of research have documented common areas of parent–child conflict, identified contexts and outcomes that correlate with conflict, and traced its developmental course over time (Arnett, 1999; Collins & Laursen, 2006; Laursen & Collins, 1994; Laursen, Coy, & Collins, 1998; Montemayor, 1986; Paikoff & Brooks-Gunn, 1991; Smetana, 2005; Steinberg, 1989; Steinberg,

2001). For example, we know that the intensity of parent–child conflict tends to increase from early to mid-adolescence and decrease or level off thereafter (De Goede, Branje, & Meeus, 2009; Kim, Conger, Lorenz, & Elder, 2001; Laursen et al., 1998; McGue, Elkins, Walden, & Iacono, 2005); that such conflict tends to occur over everyday mundane issues, such as chores and homework (e.g., Smetana, 1989; Smetana & Gains, 1999; Smetana, Yau, Restrepo, & Braeges, 1991); that conflict with sons more often revolves around behavioral problems, such as acting out or hygiene, whereas conflict with daughters more commonly involves peer group issues, such as dating or friendships (e.g., Ellis-Schwabe & Thornburg, 1986; Renk, Liljequist, Simpson, & Phares, 2005); that parent–child conflict tends to be more frequent and intense in divorced families and between step-relatives (e.g., Hetherington & Climgempeel, 1992; Hetherington, Henderson, & Reiss, 1999; Pruett, Calsyn, & Jensen, 1993); and that higher levels of parent–child conflict are associated with more child behavior problems (e.g., El-Sheikh & Elmore-Staton, 2004; El-Sheikh & Flanagan, 2001). This extensive literature demonstrates that conflict is not a peripheral aspect of family life; on the contrary, it shapes and permeates a broad range of parent–child processes.

Despite the indisputable richness of the extant literature, in this article we argue that greater insight, integration of knowledge, and empirical achievement can be realized by utilizing a powerful theory from evolutionary biology: *parent–offspring conflict theory* (POCT; Parker, Royle, & Hartley, 2002; Trivers, 1974). Although

This article was published Online First May 23, 2011.

Gabriel L. Schlomer, Norton School of Family and Consumer Sciences, Arizona Center for Research and Outreach, University of Arizona; Marco Del Giudice, Biology of Social Behavior Lab/Center for Cognitive Science, Department of Psychology, University of Turin, Turin, Italy; Bruce J. Ellis, Norton School of Family and Consumer Sciences, University of Arizona.

Gabriel L. Schlomer and Marco Del Giudice contributed equally to this article. Funding for this international collaboration was provided by the John and Doris Norton Endowment for Fathers, Parenting, and Families, Frances McClelland Institute, University of Arizona. We thank Dario Maestripieri for helpful comments on this article. We also thank Tomas Cabeza De Baca for his assistance on drafts of this article.

Correspondence concerning this article should be addressed to Gabriel L. Schlomer, Norton School of Family and Consumer Sciences, University of Arizona, McClelland Park, 650 North Park Avenue, Tucson, AZ 85721-0078, or to Marco Del Giudice, Department of Psychology, University of Turin, Via Po 14, 10123, Torino, Italy. E-mail: schlomer@email.arizona.edu or marco.delgiudice@unito.it

POCT has stimulated much empirical research and theoretical progress in the fields of animal behavior and behavioral ecology, it is barely known in the social sciences and has only rarely been applied to humans (though see Andrews, 2006; Apostolou, 2007a, 2007b; Buunk, Park, & Dubbs, 2008; Fouts, Hewlett, & Lamb, 2005; Haig, 1993; Quinlan, Quinlan, & Flinn, 2003; Schlomer, Ellis, & Garber, 2010; Soltis, 2004). Most strikingly, POCT has been almost completely ignored in the developmental literature on family conflict—the very topic to which it is most directly relevant. For example, in a review of theories and frameworks for the study of parent–child conflict, Laursen and Collins (1994) mentioned sociobiological approaches but omitted POCT. This omission is widespread. Although a cited reference search of Trivers (1974) in *Web of Science* over the last 20 years (1991–2011) generated an astounding 1008 citations, the journals *Psychological Review*, *Psychological Bulletin*, *Child Development*, *Developmental Psychology*, *Journal of Marriage and Family*, and *Journal of Family Psychology* collectively accounted for only 14 of these; none of those 14 articles used POCT to formulate and/or test hypotheses about family conflict.

This state of the science is unfortunate because POCT has far-reaching implications for understanding conflict between human children and their parents as well as between siblings. As we show here, the applications of POCT range from explaining prenatal conflict over physiological resources, to weaning conflict and its resolution, to sibling conflict over their parents' time and attention, to conflicts over adolescents' choice of sexual and romantic partners, and so on. Indeed, as we attempt to show in this review, POCT could potentially revolutionize theory and research on human parent–child conflict.

Standing in the way of such a revolution, however, are the lack of exposure to POCT within the field of human development, the relative complexity of the theory itself, and its somewhat abstract nature. The first goal of the current article, therefore, is to clearly articulate POCT for psychological scientists, both in its original formulation and more recent developments, and to draw out its implications for understanding conflict within human families. Our second goal is to connect POCT to *life history theory* (Chisholm, 1999; Roff, 1992; Sterns, 1992), an evolutionary framework describing the key developmental decisions and trade-offs in the life course of an organism, and the way these decisions are shaped by different ecological conditions. Life history theory provides a broader context for POCT and allows researchers to formulate more fine-grained and concrete hypotheses about the effects of specific ecological factors on the intensity and resolution of family conflict. In this review, we demonstrate the utility of POCT, not only for explaining what is already known about parent–child and sibling conflict but also for generating novel hypotheses, suggesting new lines of research to be followed, and moving us toward a “big picture” understanding by integrating across biological and psychological domains of knowledge.

Overview of the Article

We begin our review by summarizing the logic of POCT in a nonmathematical way. We present Trivers's (1974) seminal contribution alongside with its more recent elaborations and refinements and discuss in general terms how the theory can be applied to the human family. In the Determinants of Parental Investment

and Offspring Demand section, we place POCT in the broader ecological perspective of life history theory by reviewing the main contextual and individual factors that modulate parents' degree of investment in their offspring and offspring's demand for investment by their parents. Having laid out our theoretical background, we proceed to illustrate the application of POCT to humans in two instances of early mother–offspring interaction: prenatal conflict between pregnant mothers and fetuses (see the Prenatal Conflict section) and weaning conflict between lactating mothers and infants (see the Weaning Conflict section). We then discuss the effects of genetic relatedness on behavioral conflict between parents, children, and their siblings (see the Genetic Relatedness and Family Conflict section). In the Conflict Over Mate Choice section, we examine the small but growing literature on parent–offspring conflict (POC) over the choice of mates and spouses. Finally, in the Genomic Imprinting section, we look at POC from the perspective of maternal and paternal genes by introducing the reader to the fascinating topic of genomic imprinting and its psychological implications. We conclude with an overall assessment of the utility of POCT for developmental psychology and a review of the main opportunities and challenges for future research.

A Note on Terminology

Throughout the article, we make use of standard biological terms (such as “investment,” “allocation,” “trade-off,” etc.) to describe the dynamics of family relationships from the perspective of reproductive fitness, the ultimate currency of natural selection. We believe that psychologists should become acquainted with this terminology, as it is needed to access the biological literature; however, some clarifications are in order to avoid potential misunderstandings. To begin with, the economic connotation of these terms is no accident. Evolution by natural selection is driven by differences in reproductive success between organisms, and the evolutionary significance of any physical or behavioral trait ultimately depends on its costs and benefits with respect to the organism's fitness. Dealing with costs and benefits naturally leads to adopting economic concepts and terms. However, these terms should not be interpreted literally, and it should always be kept in mind that the *ultimate* level of reproductive fitness coexists with (and is instantiated in) the *proximate* level of behavior, motivation, emotion, and neural/physiological mechanisms. Even more importantly, economic terms do not imply that parents and children engage in conscious, deliberate calculations concerning fitness costs and benefits.

Consider *parental investment*, a term that recurs often throughout the article. Parental investment is defined as “any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring” (Trivers, 1972, p. 139). Parental investment usually involves the use of some resource (e.g., food, energy, or time), but it can also take other forms, such as protection from predators and other sources of danger (for extensive discussion of parental investment in humans, see Sear, 2011). Evolutionary biologists and psychologists analyze the dynamics of parental investment to help explain and predict affective and behavioral processes within families. For example, 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 in the arms of a loving parent have all been shaped by natural selection to obtain 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). However, this does not imply that the mother and the child are performing conscious calculations of the fitness costs and benefits of their behavior, or that they see their behavior as motivated by fitness maximization. The two levels of analysis—proximate and ultimate—are complementary but distinct and must not be confused with one another (for in-depth discussion of this topic, see Scott-Phillips, Dickins, & West, 2011).

The Logic of POCT

The insight that led Trivers (1974) to realize the inevitability of within-family conflict of interest was nothing short of revolutionary, yet it can be explained in simple terms. The easiest way to present the theory is to start from Hamilton's (1964) rule, the basic formulation of kin selection theory. Altruistic behavior (i.e., behavior that benefits another individual at a cost for the individual performing it) will evolve by natural selection only if

$$rB > C,$$

that is, if net benefit in reproductive fitness gained by the recipient (B), discounted by the relatedness between actor and recipient (r), exceeds the fitness cost to the actor (C). The relatedness coefficient r ranges from 0 to 1 and represents the probability that, through common descent, two individuals share the same allele at any given locus; for example, in diploid species, the relatedness between a parent and an offspring is $r = .5$, because (with Mendelian transmission) an allele present in one of the parents has a 50% probability of ending up in a given offspring. In total, across all genetic loci, parents and offspring can be expected to share the same alleles by descent 50% of the times.¹

The higher the relatedness coefficient r between two organisms, the more they will be selected to behave altruistically toward one another (i.e., to pay higher costs to benefit the other individual). Imagine that a mother is able to invest a certain quantity of resources in her offspring (for simplicity, we can assume offspring to be all full siblings). Resources may include food, time, active protection, and in general anything that imposes a net fitness cost on the mother by reducing her future reproductive success (e.g., because of energy expenditure, nutrient depletion, injury risk, etc.). How should she distribute these resources among the offspring? The relatedness between the mother and each of her offspring is exactly the same ($r = .5$); it follows, therefore, that all else being equal, the mother should distribute her parental investment *equally* among her offspring, with each offspring receiving the same amount of resources. The underlying logic is quite different, however, if one looks at the same decision from the perspective of a given offspring. Whereas an offspring's relatedness with each of its siblings is $r = .5$, the same offspring is perfectly related to *itself* ($r = 1.0$). It follows that each offspring is selected to demand a greater (disproportionate) share of parental investment for itself, relative to its siblings, than parents have been selected to give, thus setting the stage for parent–child and child–child conflict over the distribution of parental investment.

It is important to note that conflict in this sense does not necessarily refer to observable behavioral conflict. Rather, conflict is defined more generally in terms of a conflict of interest between parent and child. This may or may not result in behaviors that are commonly labeled as conflictual (e.g., fighting, arguing, crying, punishment, etc.). Indeed, in some cases, POC may be played out and resolved entirely by physiological means (with no behavior involved at all), as in mother–fetus conflict over fetal nutrition (see the Prenatal Conflict section).

The essence of POCT lies precisely in the difference between (a) the optimal parental investment from the parent's perspective and (b) the optimal parental investment from the perspective of the offspring. Trivers's (1974) model thus predicts that natural selection will maintain a conflictual tension within families concerning the allocation of parental investment. Further, the theory can be easily extended beyond direct parental investment; indeed, as noted by Trivers, *any* behavior that results in a cost to the parent and a benefit to an offspring (e.g., the offspring's decisions concerning mating and reproduction, provided they can affect the parent's fitness in some way; see the Conflict Over Mate Choice section) has the potential to become an arena of within-family conflict. Accordingly, POCT has deep and wide-ranging implications for the study of social behavior.

The Analysis of POCT

For over 30 years, biologists have employed and extended Trivers's (1974) seminal model to better understand what factors affect the intensity and outcomes of within-family conflict in animals. In this section, we provide the reader with a concise overview of the current state of the theory (for extended discussion, see Godfray, 2002; Parker et al., 2002; Royle, Hartley, & Parker, 2004). There are two main kinds of POC models. The simplest (and oldest) models are called *battleground models*; they seek to quantify the extent of conflict and explain how potential conflict intensity varies as a function of the ecological characteristics of a given species or population. *Resolution models* go one step further and seek to predict how the conflict will in fact be resolved: Will the parent “win,” or will a compromise be reached? And if so, how much will the outcome deviate from the parent's and the offspring's respective optima?

Conflict Battleground

Although Trivers's (1974) original model demonstrates that parents and offspring will generally disagree about the optimal level of parental investment, the intensity of conflict at the behavioral and physiological level should depend on *how much* they disagree (i.e., on the gap between the parental and the offspring optima). Further, battleground models (e.g., Parker, 1985; Trivers,

¹ By this simplified account, the relatedness coefficient r can be treated 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. 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 defined as a regression coefficient and can take negative values (see Grafen, 1985).

1974) can be used to characterize the ecological factors that increase (or decrease) the extent of POC. To determine the conflict battleground, however, it is crucial to distinguish two forms of competition between siblings: *intra-brood* and *inter-brood* competition.

Intra-brood competition occurs between multiple young that are dependent at the same time (e.g., pups in the same litter), when parental investment is a fixed amount that has to be distributed among siblings. In this case, the extent of conflict is expected to depend on the available level of resources (less resources, more conflict), on the number of offspring competing for those resources (more offspring, more conflict), and, crucially, on the relatedness between siblings. Conflict is minimized when siblings are always full siblings ($r = .5$); however, under any degree of multiple paternity (due, e.g., to polygamy or cuckoldry), the average relatedness decreases, up to the point where all of one's siblings can be expected to be half-siblings ($r = .25$), which maximizes conflict. For example, in a comprehensive study of passerine birds, Briskie, Naugler, and Leech (1994) found a negative correlation between begging intensity and genetic relatedness among siblings: In species where the genetic relatedness between siblings was generally low, offspring begged louder. This finding persisted even after controlling for the potential confounding effects of nestling size, nestling number, and variation in paternal care. In total, by straightforward application of Hamilton's (1964) rule, decreasing relatedness between siblings tends to increase the extent of POC.

Inter-brood competition. Even if a parent only has one dependent offspring at a time (and, thus, there is no intra-brood competition), the offspring is still competing for increased investment, only this time with its *future* siblings. Increased parental investment in the present offspring inevitably decreases the amount of investment that the parent will be able to provide to future offspring. The extent of POC resulting from inter-brood competition does not depend directly on the relatedness between siblings (Parker, 1985; Lessells & Parker, 1999) but on a more complex parameter that is determined by the organism's mating system: the *interdependence* between the mother's and the father's reproductive success.

To the extent that the fitness opportunities and costs experienced by one parent are linked to the fitness opportunities and costs experienced by the other parent, the two are *interdependent* (constrained). This may happen, for example, in a mating system where mates are scarce, and if one partner dies, the other will have trouble finding another mate (thus incurring a fitness cost). More generally, interdependence is increased when investment by one of the parents translates into a fitness cost for the other parent (e.g., in species where males protect nursing females from predators and experience fitness costs as a consequence). The lowest levels of inter-brood competition are predicted in mating systems where individuals have only one mate over the course of their lifespan, with no replacement even if one of the partners dies (so-called "true monogamy"). In this context, the parents are maximally interdependent.

In the simplest case when only the mother provides parental investment, an individual offspring can maximize its fitness by extracting a higher amount of investment from the mother. If the costs paid by the mother do not affect the future reproductive success of the father (independence), the offspring will be selected to extract more maternal investment—as it can "offset" the in-

creased cost paid by the mother through the father's reproduction with other females. If, however, the father itself pays a cost associated with increased maternal investment (interdependence), the offspring cannot compensate for the fitness cost paid by the mother through its father's reproduction. As a result, it will settle for a lower level of maternal investment, thus reducing the gap between parental and offspring optima and the intensity of conflict. Thus, conflict intensity is predicted to increase when the reproductive success of fathers is independent from that of mothers, and vice versa; this will happen more frequently in polygynous or promiscuous mating systems, but reproductive independence can coexist with monogamy if parents can easily "replace" their current mate without paying additional costs (see Lessells & Parker, 1999; Parker et al., 2002). Finally, the dynamics of inter-brood competition may depend on specific patterns of genetic expression in the offspring—a case in point is that of imprinted genes, that is, genes whose pattern of expression depends on their parent of origin (see the Genomic Imprinting section).

Although intra-brood and inter-brood competition are conceptually distinct and can be discussed separately for clarity, they are not mutually exclusive, and a reproductive system can involve a combination of both. This is the case for humans, whose families typically include multiple dependent children of different ages. In human families, each child is competing for investment with his/her future siblings (inter-brood). True monogamy is virtually nonexistent in human societies (Barash & Lipton, 2001), and most mating systems allow for multiple partners (especially for men); thus, the interdependence between mothers and fathers is expected to be variable but far from complete, and inter-brood competition can be expected to be a significant source of POC in humans. In addition, older children are competing with their younger siblings for the parents' attention and resources (intra-brood). It is important to note that, because of the extended period of immaturity in humans, intra-brood conflict will often concern *different* resources for the two competing siblings. For example, a 4-year-old boy is not directly competing with his 6-month brother for the mother's milk; however, the time spent lactating and the energy devoted to milk production do reduce the mother's capacity to take care of the older child, protect him, prepare food for him, and so on.

Conflict Resolution

Whereas the extent of potential conflict is predicated on relatively general family and ecological factors (e.g., between-sibling relatedness, family size, resource availability, mating systems), predicting the outcome of conflict requires more detailed assumptions about the actual mechanisms that regulate parental investment. This is extremely valuable because, in contrast to simple battleground models, resolution models permit (at least in principle) formulation of precise quantitative predictions (Godfray, 2002). Early models focused on who (parent or offspring) gets to control the allocation of resources. At one extreme of the power continuum are sibling competition models (e.g., Parker, 1985; Parker & Macnair, 1979). These models assume that offspring totally control the allocation of parental investment among sibling (e.g., by fighting for access to the best feeding position); accordingly, asymmetries in competitive ability between siblings determine the distribution of investment. However, even sibling competition models do not assume that the more competitively

advantaged sibling will try to monopolize all of the parental investment. Indeed, all else being equal, Sibling A can maximize her fitness by monopolizing parental investment only until her marginal gains fall to half that of Sibling B (presuming B is a full sibling with whom A has a relatedness of .50; see Parker et al., 2002). In family contexts in which there are multiple dependent siblings of different ages, as is commonly the case in human families, the marginal gains of the older sibling may quickly fall to below 50% of that of the younger sibling, given that the fitness return on parental investment may be much higher for relatively helpless young children. Indeed, older siblings must eventually be weaned of parental support and may even become “helpers at the nest,” promoting the fitness of their younger siblings.

In sibling competition models, POC (reflecting both intra- and inter-brood competition) is ultimately resolved by a compromise between parental and offspring optima (i.e., parents invest more than their optimal amount but still less than the offspring optimum). At the other extreme, “honest signaling” models assume that parents have complete control over investment, and offspring merely signal their current level of need by some kind of costly signals. Allocation is then determined by siblings’ relative need. Fitness costs associated with signaling (e.g., loud begging may be costly because it is metabolically expensive, or because it attracts predators) permit a reliable communication system to evolve, by offsetting the potential benefits of exaggerated or deceptive signals (Zahavi & Zahavi, 1997). In some signaling models (e.g., Godfray, 1991, 2002), the conflict is resolved at the parental optimum, whereas in others (Johnstone, 1996), a compromise is reached between parental and offspring optima, depending on the specific assumptions made in the models. A great deal of empirical research in various animal species has been conducted with the aim of discriminating between these competing models (see Royle et al., 2004, for review).

Another way to approach conflict resolution is to focus not on who controls resource allocation, but rather on the empirical functions that describe the reciprocal influence between parent and offspring: the effect of demand on supply (how the parent adjusts investment levels in relation to changes in offspring demand) and the effect of supply on demand (how offspring solicitation is affected by changes in parental investment). Parker and colleagues (Parker et al., 2002; Royle et al., 2004) showed that the critical parameter predicting the conflict outcome is the effect of supply on demand. If changes in parental investment do not affect solicitation level (i.e., the effect of supply on demand has a slope equal to zero), the conflict is resolved at the parental optimum; if instead offspring solicitation diminishes when parental investment increases (i.e., the effect of supply on demand has a negative slope), the conflict is resolved at a compromise level. In some cases, increased parental investment may elicit increased demands from offspring (i.e., the effect of supply on demand has a positive slope); mathematical models then predict that conflict should be resolved at an investment level even lower than the parental optimum. All three mechanisms have been documented empirically, although negative slopes appear to be more common than the other two types (Royle et al., 2004; for an example of how the functions describing the effect of supply on demand and the effect of demand on supply can be mapped by means of systematic experimentation, see Kölliker, 2003).

There has been surprisingly little research on how POC resolution models apply to human families. It is likely, however, that different types of investment can give rise to different conflict scenarios. For example, humans typically breast-feed only one infant at a time; thus, signaling models are more relevant to conflicts about lactation and weaning (see the Weaning Conflict section). By contrast, older children can fight over food shares, making sibling competition for food a more plausible scenario, at least in some ecological contexts. No systematic attempts have been made to map the general effect of supply on demand in human children; again, it is quite possible that the shape of the function depends on the specific type of investment concerned. Even in absence of targeted data, we can use the findings of developmental psychology to derive some plausible hypotheses about the shape of the effect of supply on demand. A good example is attachment theory, which deals with rather general dimensions of parental investment, operationalized as sensitivity, availability, and emotional warmth (Ainsworth, Blehar, Waters, & Wall, 1978; Cassidy & Shaver, 2008). The lowest demands on parents are those of avoidant children, who experience rejecting and insensitive parenting (i.e., cues of low investment) and go on to develop a distancing, self-reliant coping style. Securely attached children (who experience the highest levels of investment) demand more than avoidant ones. However, the strongest demands for investment come from ambivalent children, who experience inconsistently sensitive caregivers (i.e., intermediate parental investment) and display clingy, attention-seeking, and overly dependent behavior. This points to a nonlinear, inverted-U shape of the effect of supply on demand; the outcome of conflict resolution would then vary along the investment continuum, depending on the local slope of the curve. Of course, this example does not prove that the effect of supply on demand in human children has this specific shape; rather, it is meant to illustrate how extant psychological data can be brought to bear on POC models, and how POCT can orient researchers toward new types of empirical questions.

Determinants of Parental Investment and Offspring Demand

Imagine a working class family, the Knights, with three children: Alicia (age 3), Kayla (age 11), and Ryan (age 16). They are considering a fourth child (Maybebaby). The Knights have enough resources to keep all three of their current children alive, but additional investments to increase the fitness of one child would force trade-offs that diminish the fitness of other children. For example, if the parents buy Ryan the car, hi-tech gadgets, and clothing that he needs to climb the social hierarchy at his high school and attract mates (factors that may considerably influence his long-term social and reproductive trajectories; Ellis et al., 2011), they will have to put Alicia into lower quality daycare and forgo Maybebaby. What factors regulate how parents make these kinds of resource allocation decisions? At the same time, Alicia, Kayla, and Ryan need to modulate their own demands for parental investment. For example, if Alicia requires too much time and resources from her parents, enhancing her own health and competitive abilities, it will close the door on Maybebaby and cause Kayla to be neglected as she enters the vulnerable pubertal transition. What factors influence how intensely children solicit parental investment?

As reviewed in the previous section, POCT explains conflict within families arising from the divergence between (a) parental strategies for allocation of resources (i.e., the optimal levels of investment that parents are selected to devote to each offspring, current and future) and (b) offspring demand for parental resources (i.e., the optimal levels of investment that offspring are selected to solicit or extract from parents). POCT addresses this conflict in general and abstract terms and points to a limited number of factors (such as relatedness between siblings, or the total amount of resources available to parents) that can influence conflict intensity. However, many ecological and individual factors converge to influence parental strategies for allocating resources vis-a-vis offspring strategies for soliciting and extracting parental investment. Using life history theory as an organizing framework, this section provides an overview of these factors and their interplay in setting the stage for conflict dynamics.

Parental Reproductive Strategy

From the parent’s perspective, the critical decision concerns the amount of resources that will be devoted to a given offspring. As shown in Figure 1, for a number of reasons—species-typical mating systems and availability of mates, impact of parental investment on offspring fitness, paternity certainty, harshness and unpredictability of local environments, parental age, parental condition/resources, genetic variation—parents differ in their reproductive strategies (e.g., Ellis, Figueredo, Brumbach, & Schlomer, 2009; Nettle, 2010; Quinlan, 2007). These differences occur on two dimensions that directly affect offspring: current versus future reproduction and quantity versus quality of offspring (see Figure 1).

According to life history theory (Chisholm, 1999; Roff, 1992; Sterns, 1992), the most fundamental trade-off faced by parents is between current and future reproduction. Effort put into reproducing now will use energy or resources that cannot be used or saved

for future reproduction. The organism therefore faces the risk of crossing an investment threshold, above which resources consumed in support of current reproduction would have produced better fitness returns if they had instead been allocated to future reproduction (Chisholm, 1999). The costs of current reproduction may be paid in terms of reduced number, quality, or survival of future offspring, as well as reduced growth and survival of the parent. The greater the parent’s probability of breeding again in the future, the more parents can be expected to withhold resources from current reproduction, and thus the greater the potential for conflict with extant offspring (in Figure 1, see the mediated path “parental reproductive strategy” → “total parental investment in current offspring” → “parental investment in individual offspring” → “offspring solicitation/demand for investment”). Further, conflict should increase as a function of reduced interdependence between maternal and paternal reproductive success and reduced relatedness between siblings (see The Logic of POCT section), both of which depend on parental reproductive strategies and on the current mating system. These relations are shown in Figure 1 in the mediated paths from “mating system/mate availability” and “parental reproductive strategy” to “offspring solicitation/demand for parental investment” through “parental interdependence” and “sibling relatedness.”

At the most basic level, trade-offs between current versus future reproduction are influenced by energetic conditions—caloric intake, energy expenditures, and related health conditions—which set a baseline for many developmental and reproductive processes, including amount and duration of parental investment. As reviewed in Kuzawa (2005) and Ellison (2001), poor energetic conditions translate into development of a more energy-sparing phenotype: slower growth, delayed sexual maturation, low gonadal steroid production, small adult body size, reduced fecundity, and lower maternal milk production in mammals. Along these lines, small body size, wide birth spacing, monogamous marriage, and

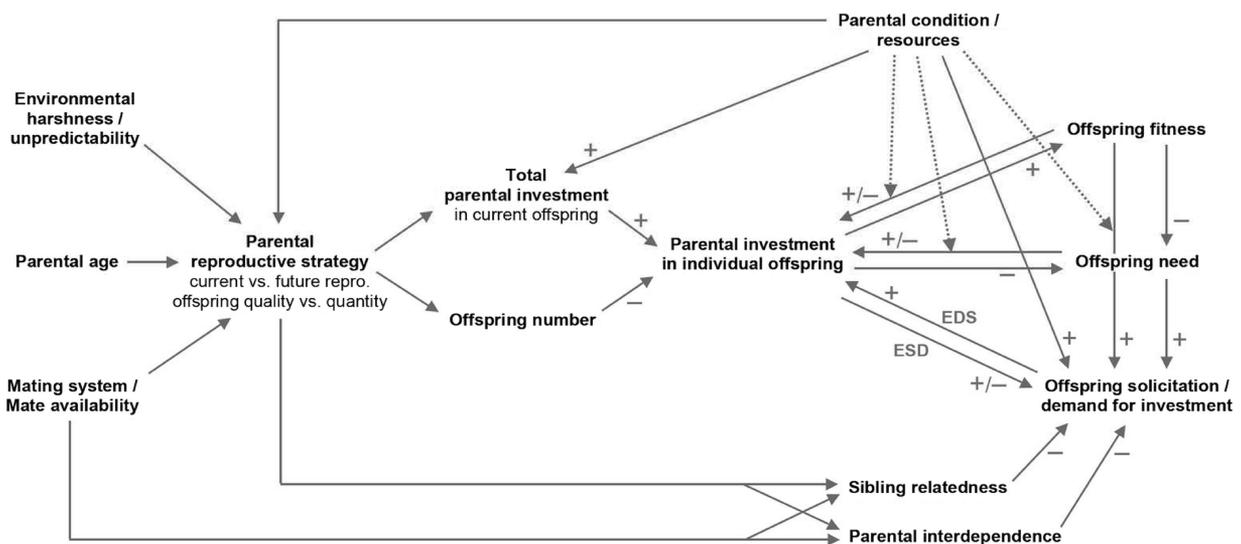


Figure 1. Factors regulating parental investment and offspring demand. Dotted lines indicate moderation effects. The pattern of relations depicted in this figure is explicated in the Determinants of Parental Investment and Offspring Demand section. EDS = effect of demand on supply; ESD = effect of supply on demand.

father-present social systems are more likely to be found among human hunter-gatherers inhabiting harsh ecologies where biparental care (male provisioning) is substantial and important for offspring survival and reproductive success (Draper & Harpending, 1988; Geary, 2000; Kaplan & Lancaster, 2003, Table 7–1; Marlowe, 2003).

Prolonged and intensive investment in current offspring occurs at the expense of investment in future offspring. When resources are scarce, parents may sacrifice future reproduction by extending investment in current offspring for longer than under ideal conditions (Bateson, 1994; see Figure 1: “parental reproductive strategy” → “total parental investment in current offspring”). For example, under normal conditions spotted hyena mothers wean their offspring at approximately 12 months of age but often delay weaning until 18 months of age in habitats characterized by low or fluctuating availability of prey (Hofer & East, 1995). In total, mothers tend to monitor and strategically respond (depending on their own resources/condition) to the progress and condition of their current offspring (Bateson, 1994; see Figure 1: effects of “offspring need” and “offspring fitness” on “parental investment in individual offspring,” as moderated by “parental condition/resources”). This complex web of parental investment decisions is discussed in more detail below. A key factor regulating parental investment in any given child is the likely impact of that investment on the child’s fitness (Ellis et al., 2009; Quinlan, 2007).

Closely related to current–future trade-offs are quality–quantity trade-offs. Constraints on resources and energy, both developmentally and over evolutionary time, bias organisms toward investing in either a relatively small number of “high-quality” offspring or a relatively large number of “low-quality” offspring (Sterns, 1992). In humans, allocation of resources toward high-quality offspring is often associated with monogamy and biparental investment, which lead to increased interdependence between parents. Higher quality offspring tend to have better health, survival, and developmental outcomes. To the extent that parents favor offspring quantity over quality, thus reducing investment per child, the potential for conflict with any given offspring increases. In Figure 1, this principle is illustrated by the negative effect of “offspring number” on “parental investment in individual offspring,” which in turn affects “offspring fitness,” “offspring need,” and “offspring solicitation/demand for investment.”

“Total parental investment” (maternal investment plus paternal investment) is divided among offspring to generate the level of “parental investment in individual offspring.” The effects of resource division among offspring can be demonstrated in species that produce litters. Provision of food is a critical aspect of parental investment. It follows that as litter size increases, investment in each offspring decreases, resulting in smaller and less nourished offspring. This trend has been found in many different species ranging from invertebrates to birds to mammals (see Klomp, 1970; Mendl, 1988; Trumbo, 1996). The quality–quantity trade-off is also pervasive among humans in Western societies, where larger family size is associated with less direct parental involvement in key childcare activities (Lawson & Mace, 2009), and in preindustrial societies, where larger family size has been linked to poorer growth and survival outcomes of offspring (e.g., Borgerhoff Mulder, 2000; Hagen, Barrett, & Price, 2006; Strassmann & Gillespie, 2002). On the other hand, when parents are faced with unusually small litters, they may invest heavily to increase offspring quality

(Mendl, 1994). Either way, the more that parents divide resources among offspring, the greater the potential for POC.

Animals often inhabit environments that afford enough bioenergetic resources to support basic somatic functions and provisioning of offspring but are dangerous and unpredictable in other ways. Environments may be characterized by external sources of disability and death (e.g., predation, warfare, weather cycles, infectious disease) that are relatively insensitive to the adaptive decisions of the organism and/or vary unpredictably over time or space (Ellis et al., 2009). These conditions result in diminishing fitness returns on parental investment in any given offspring (above a basic level) and thus favor shifts toward offspring quantity over quality. This is captured by the arrow in Figure 1 from “environmental harshness/unpredictability” to “parental reproductive strategies.” The shift toward offspring quantity involves limiting parental investment in given offspring and is indexed empirically by such constructs as harsh, neglectful, rejecting, and insensitive parenting. As predicted by life history theory, this type of low-investment parenting is disproportionately found in dangerous and/or unpredictable environments (Ellis et al., 2009).

Offspring’s Fitness and Need

Equal division of resources among offspring rests on the assumption that all offspring are equal in their potential to survive and reproduce. This is often not the case, however, and models of POC suggest that parents may discriminate among offspring according to their *fitness* and *need*. Fitness refers to the reproductive value of offspring (i.e., their expected future reproductive success); it is signaled by such characteristics as age, size, health, and competitive ability. Need refers to the increase in fitness of offspring as a result of receiving a unit of parental investment (Royle, Hartley, & Parker, 2002). In POC models, need and fitness are assumed to be negatively related (see Figure 1), whereby offspring that display higher fitness have less need for parental provisioning than do their younger, weaker, or less healthy siblings. As shown in Figure 1, “offspring fitness” has a bidirectional relation with parental investment. On the one hand, parental investment tends to reduce the offspring’s need and to increase their fitness. On the other hand, offspring fitness influences the resource allocation decisions of parents. In particular, parental investment in any given offspring should only continue until the fitness gains achieved through continued investment become less than the potential gains that could be realized through investment in other (current or future) offspring (Roff, 1992; Sterns, 1992). Further, parents should be selected to cease investment altogether when offspring are in a very poor state (and thus unlikely to survive) and when conditions are sufficiently variable that they can be expected to improve for future reproduction (Bateson, 1994).

This prediction has been supported by cross-cultural data demonstrating that parent-inflicted infanticide in humans occurs overwhelmingly when the child is unlikely to survive because of poor health or unfavorable circumstances external to the child (Daly & Wilson, 1988; reviewed in Soltis, 2004). A powerful external circumstance that regulates parental investment is resource availability: lack of nutritional and economic resources restricts investment in any given child (see Figure 1: “parental condition/resources” → “total parental investment in current offspring”). Above and beyond the effects of resource availability, however,

children who are mentally, physically, or behaviorally atypical—and thus are unlikely to achieve reproductive success—suffer dramatically elevated rates of child abuse and neglect (Daly & Wilson, 1980; reviewed in Bugental & Happaney, 2004; Soltis, 2004). These effects, which are pervasive across time and culture, are captured by the arrow in Figure 1 from “offspring fitness” to “parental investment in individual offspring.”

Resource-scarce environments force parents to make strategic allocation decisions in partitioning their investment among offspring. These resource allocation decisions, which have been studied most extensively in birds, show a consistent pattern: When energetic resources are scarce, parents tend to favor larger, more competitive offspring and sometimes selectively starve smaller, depleted offspring (e.g., Gottlander, 1987; Kilner, 1995; Leonard & Horn, 1996; Moreno-Rueda, Soler, Soler, Martínez, & Pérez-Contreras, 2007; Stamps, Clark, Arrowood, & Kus, 1985; Whittingham, Dunn, & Clotfelter, 2003; reviewed in Royle et al., 2004). In Figure 1, this effect is captured by the moderating effect of “parental condition/resources” on the arrows going from “offspring fitness” and “offspring need” to “parental investment in individual offspring.”

Available evidence suggests that humans follow a similar pattern, particularly in ecological contexts that force parents to make tough reproductive choices. Across a sample of traditional societies in the Human Relations Area Files, either having too many children or births spaced too closely together was a common motive for infanticide; when this occurred, it was always the younger child who was killed rather than an older, more reproductively valuable sibling (Daly & Wilson, 1988). Likewise, under extreme socioeconomic conditions, such as in Brazilian shantytowns where child mortality rates are very high, mothers have been found to treat their offspring differentially on the basis of their perceived survival prospects, investing in vigorous, healthy infants while selectively neglecting others (Scheper-Hughes, 1992; for extensive discussion of these issues, see Hrdy, 1999).

By contrast, in stable and well-resourced environments, parents can afford to invest in needier offspring in a “compensatory” fashion (e.g., Stamps et al., 1985). In humans, parents may devote extra time and attention to needier children—when they can afford to do so. Among the Karo Batak of North Sumatra, for example, children with greater need and/or lower fitness (indexed by younger age and higher propensity to illness) tend to cry and whimper more often (Kushnick, 2009); in turn, this observed fussiness predicts a greater frequency of nursing (see Figure 1: “offspring solicitation/demand for parental investment” → “parental investment in individual offspring”), a pattern consistent with a positive effect of demand on supply function (the default assumption of POC models). Interestingly, longer feeding periods were followed by *increased* fussiness, suggesting a positive effect of supply on demand function whereby increasing investment increases solicitation (see Figure 1: “investment in individual offspring” → “offspring solicitation/demand for investment”). As the authors note, this is a rather crude assessment of the effect of supply on demand function, which can only be elucidated through systematic experimental work; however, these results provide a useful starting point for future research and show how POCT can be used to inform both research design and data interpretation.

In general, the dilemma faced by parents is whether to invest heavily in high-risk children to improve their chances of survival

and reproduction or to focus resources on current (or future) offspring with the highest reproductive value (Mann, 1992). Mothers in Western societies from higher socioeconomic backgrounds—who have less to lose from investing in high-risk offspring—do not necessarily provide less care for high-risk children (such as low birth weight or premature infants); however, mothers do show behavioral preferences for healthier children (e.g., more holding, touching, soothing, and smiling), nurse them for longer periods of time, and wait longer before having their next child (Barratt, Roach, & Leavitt, 1996; Bereczkei & Csanaky, 2001; Goldberg, Perrotta, Minde, & Corter, 1986; Mann, 1992; Robson & Cline, 1998). In total, mothers are more likely to enhance the fitness of current healthy offspring, compared with high-risk offspring, at a cost to future reproduction.

However, the effect of “offspring fitness” on “parental investment in individual offspring” may be moderated by “parental condition/resources” (as shown in Figure 1). This hypothesis has been tested on predominantly Latina samples in the United States. As predicted, mothers in better condition or with more interpersonal resources (i.e., absence of depression, participation in a parenting skills program) disproportionately invested in high-risk versus low-risk infants and young children, whereas mothers in worse condition or with fewer interpersonal resources (i.e., presence of depression, no experimental enhancement of parenting skills) showed the opposite pattern (Beaulieu & Bugental, 2008; Bugental, Beaulieu, & Silbert-Geiger, 2010).

Parent’s Age

According to the *terminal investment hypothesis* (Fisher, 1930; Williams, 1966), when future reproductive potential is low, and thus conserving resources for future reproduction is likely to result in wasted effort, organisms should invest heavily in already-born offspring (current reproduction). Such an increase in investment should reduce POC by leading to greater convergence between parental and offspring optima and eliminating inter-brood competition. This series of relations is represented in Figure 1 by the mediated path “parental age” → “parental reproductive strategy” (reflecting the current–future trade-off) → “total parental investment in current offspring” → “parent investment in individual offspring” → “offspring solicitation/demand for investment.” In females, the likelihood of successful future reproduction depends strongly on age, leading to the hypothesis that investment in current offspring should be relatively low among young mothers and should increase with age.

Empirical tests of this hypothesis in the animal literature have yielded mixed results, in part because many studies do not consider the increasing costs associated with parental investment as an organism ages (Clutton-Brock, 1984). Tests of the terminal investment hypothesis in mammals have proven complex, and results are often equivocal (e.g., Hoffman, Higham, Mas-Rivera, Ayala, & Maestripieri, 2010; Weladji et al., 2010). In addition, some debate exists regarding the effects of age versus parity (number of births)—two confounded aspects of female development—on parental investment (Fessler, Navarrete, Hopkins, & Izard, 2005; though see Braza, 2004). However, the relationship between age and investment has been extensively studied in the California gull (*Larus californicus*; Pugesek, 1990, 1995; Pugesek & Diem, 1990). This corpus of research shows (a) that older gull mothers

withhold food from nestlings less and have longer periods of investment and (b) that increased investment is not a product of increased foraging efficiency with age. This relationship between age and investment is not linear, however; Pugesek and Diem (1990) found that indicators of investment peaked among gulls 16–19 years of age and then declined among gulls 20–23 years of age.

The human literature shows both curvilinear and linear effects of maternal age on investment in offspring. Prenatally, these effects appear to be curvilinear. Specifically, maternal investment in fetal development (as measured by infant birth weight) peaks among women 25–29 years of age and then declines thereafter (Braza, 2004). This effect was not explained by the parity of the mothers. Postnatally, however, maternal investment appears to increase linearly with maternal age. On the one hand, young mothers are most likely to neglect, abuse, or kill their young children (J. Brown, Cohen, Johnson, & Salzinger, 1998; Luke & Brown, 2007; Mersky, Berger, Reynolds, & Gromoske, 2009; Overpeck, Brenner, Trumble, Trifiletti, & Berendes, 1998). On the other hand, positive forms of investment in offspring tend to increase as mothers age. For example, in a study of 4-month-old infants, older mothers tended to be more satisfied in their role as a parent and spent less time away from their child (Ragozin, Basham, Crnic, Greenberg, & Robinson, 1982). These effects were not explained by maternal education, parity, gestational age, or income. Furthermore, compared with younger mothers, older mothers tended to be more sensitive to infant cues, particularly among primiparous mothers (Ragozin et al., 1982). Even after controlling for socioeconomic status, maternal education, ethnicity, intelligence, social desirability of responding, and child age and language competence, older mothers directed more praise and physical affection toward their toddlers than did younger mothers (Bornstein & Putnick, 2007). Finally, older mothers have been found to be especially likely to tolerate and invest in needy offspring (Beaulieu & Bugental, 2008).

From the perspective of POCT, this higher level of parental investment among older mothers should result in reduced parent–child conflict. To our knowledge, however, this prediction has not been tested as yet. An important direction for future research will be to examine the moderating influence of parental age on various patterns of parent–child conflict.

Child-Specific Influences on Offspring Solicitation/Demand for Investment

Several additional factors are expected to influence the amount of investment demanded by a given offspring. At the most basic level, POCT predicts that “offspring solicitation/demand for parental investment” will increase as biological relatedness between siblings decreases (see The Logic of POCT section). Specifically, within families, Sibling A can maximize her fitness by monopolizing parental investment until her marginal gains fall to half that of Sibling B (if Sibling B is a full sibling with whom she has a relatedness of .50) or to one fourth that of Sibling B (if Sibling B is a half sibling with whom she has a relatedness of .25; Parker et al., 2002). This effect, as depicted in Figure 1 (“sibling relatedness” → “offspring solicitation/demand for investment”), is reviewed in detail in the Genetic Relatedness and Family Conflict section.

At the same time, offspring need to modulate their demands for parental investment in relation to parental condition/resources. As discussed by Bateson (1994), whereas increased levels of solicitation among very young offspring generally increase offspring survival in the short-term, the strength of this relation decreases as offspring get older. Further, depending on parental condition/resources, too much demand for investment early in childhood may reduce the capacity of parents to provide necessary investment in the future. Thus, offspring should monitor parental condition/resources and adjust demands accordingly (Bateson, 1994), so as not to seriously endanger the health of the nursing mother (see Figure 1: “parental condition/resources” → “offspring solicitation/demand for investment”). This is especially relevant for species, such as humans, with extensive postweaning parental investment.

In addition, “offspring solicitation/demand for investment” should be modulated by “parental condition/resources” relative to the “need” and “fitness” of different siblings. Just as parents tend to favor larger, more competitive offspring when energetic resources are scarce (reviewed above), more competitively advantaged (dominant) siblings tend to monopolize parental investment under conditions of resource scarcity but *not* under conditions of resource abundance (see Figure 1: “offspring fitness” → “offspring solicitation/demand for parental investment,” as moderated by “parental condition/resources”). This discriminative pattern of sibling competition and demand has been documented across ecologically and taxonomically diverse species (including a wide range of avian species [reviewed in Drummond, 2001], spotted hyenas [Hofer & East, 2008; White, 2008], and Galápagos fur seals and sea lions [Trillmich & Wolf, 2008]). Although this pattern of competitively advantaged siblings monopolizing scarce parental resources often inflicts extreme costs, including death, on competitively disadvantaged siblings, mathematical models have demonstrated that this behavior could still evolve if the fitness benefits accrued by the dominant sibling exceed the costs incurred by loss of a sibling (with that cost discounted by the coefficient of relatedness r ; Parker, Mock, & Lamey, 1989). Such behavior should be conditionally expressed, however, developing when resources are so scarce that parents cannot adequately feed all members of a brood. In this context, the dominant sibling, to ensure its own growth and survival, can benefit from selfishly consuming a disproportionate share of the food; by contrast, given sufficient energetic resources, the small gain in growth and survival obtained by eliminating or devaluing siblings is outweighed by the cost to inclusive fitness (Hofer & East, 2008). These documented effects of resource scarcity on sibling competition for parental investment suggest an important direction for future research on sibling rivalry in humans.

Summary

The amount of investment that parents allocate toward a given offspring, on the one hand, and the levels of offspring solicitation and demand for parental investment, on the other, are multiply determined. Parental investment depends on the parents’ reproductive strategy, parental age, parental condition/resources, number of offspring, and on parental assessments of the need and fitness of different offspring. Offspring solicitation/demand depends fundamentally on the level of parental investment they are receiving

together with offspring fitness, offspring need, number of siblings, genetic relatedness among siblings, interdependence between parents, and parental condition/resources. These factors regulating parental investment and offspring demand interact to modulate the intensity of parent-child conflict, which ultimately reflects the gap between parent's and offspring's optimal levels of parental investment.

Prenatal Conflict

In humans, the most extensive applications of POCT have been to parent-child conflict before birth. The fetal stage is increasingly recognized as an important phase in the human life cycle. The processes that unfold before birth set the stage for later development and have far-reaching implications for physical and psychological health in childhood and even adulthood (Bateson et al., 2004; Kuzawa, 2007). During prenatal development, the interaction between fetal and maternal physiology affects fetal growth rate and birth weight (with their many consequences for physical and cognitive development; see Kuzawa, 2007; McCarton, Wallace, Divon, & Vaughan, 1996; Wilcox, 2001). Even more importantly, maternal hormones can exert powerful effects on the calibration of the child's metabolism (e.g., Gluckman, Hanson, & Beedle, 2007), temperamental reactivity (e.g., Huizink, de Medina, Mulder, Visser, & Buitelaar, 2002; Möhler, Parzer, Brunner, Weibel, & Resch, 2006), and even future psychopathology risk (e.g., Khashan et al., 2008; Van den Bergh & Marcoen, 2004; Van den Bergh, Mulder, Mennes, & Glover, 2005).

Despite the growing attention to fetal development, most researchers still adopt an outdated view of pregnancy as an essentially harmonious and cooperative enterprise, quite unlike the rewarding but often conflictual relationships that later take place between parents and their infants/children. However, POC is already present (and arguably quite intense) well before birth. As Trivers (1974) noted: "Since parental investment begins before eggs are laid or young are born . . . I assume that parent-offspring conflict may in theory begin as early as meiosis" (p. 252). In fact, later research has uncovered a world of strategic parent-offspring relations before birth involving a complex mixture of cooperation and competition (Haig, 1993). In this section, we focus on the main conflicts that take place during human pregnancy and explore their implications for psychological research.

Fetal Nutrition and Growth

Human pregnancy involves a long, sustained period of maternal investment, and it puts a remarkable physiological burden on the woman (Ellison, 2001). The most obvious form of maternal investment is the provision of nutrients to the fetus, which in humans takes place through the placental circulatory system. Maternal blood enters the placenta through spiral arteries and exchanges nutrients and oxygen with fetal blood through the placental barrier. This mechanism implies two possible conflicts between the mother and the fetus: the conflict about *blood flow* (the more blood enters the placenta, the more nutrients are transferred to the fetus) and the conflict about *nutrient concentration*, in particular that of blood glucose.

One of the most puzzling aspects of gestation is the marked inefficiency in how circulation is regulated. Cardiac output rises

dramatically early in pregnancy and remains elevated until the third trimester; at the same time, vasodilation occurs, lowering arterial resistance during the first and second trimesters. The net effect is a drop in blood pressure in early and mid-pregnancy, with pressure typically rising again during the third trimester (Easterling, Benedetti, Schmucker, & Millard, 1990). Vasodilation appears to put an unnecessary strain on the mother's heart, because an effective system would increase blood supply to the placenta by *increasing* arterial resistance (vasoconstriction), thus elevating blood pressure with only a modest amount of increase in cardiac output. In fact, maternal vasodilation can be explained as a defense of mothers against fetal release of factors that induce constriction of maternal vessels. Because placental arteries have extremely low resistance, increasing maternal blood pressure benefits the fetus by directly increasing placental flow (Haig, 1993). The side effects of this physiological tug-of-war are (a) the apparent inefficiency of the system and (b) the occasional risk of fetal-induced maternal hypertension. In accord with the conflict model, gestational hypertension can be harmful to the mother but predicts *lower* perinatal mortality in the fetus and higher birth weight (Langer, Yogev, Most, & Xenakis, 2005). This is especially true when hypertension is not associated with proteinuria, also known as preeclampsia, and is considerably more dangerous for the fetus as well as for the mother (Lindheimer, Taler, & Cunningham, 2008; Moore & Redman, 1983; Ros, Cnattingius, & Lipworth, 1998; Symonds, 1980).

Glucose and insulin levels in mothers are altered during pregnancy. Glucose concentration at baseline drops early in pregnancy, stabilizing to the new lower level by end of the first trimester (Lind & Aspillaga, 1988). Maternal insulin levels and insulin response after meals remain low until mid-gestation but rise dramatically during the third trimester. At the same time, insulin resistance develops, leading to longer elevation of blood sugar after meals. The combination of high insulin levels and insulin resistance is another apparent paradox, which again can be explained by underlying POC (Haig, 1993). The most abundant hormone produced by the placenta is human placental lactogen. Through human placental lactogen secretion, the fetus is able to induce insulin resistance in the mother, most likely by activating prolactin receptors. The rise in maternal insulin levels during the third trimester can be interpreted as a countermeasure against fetal manipulation, and the same is true for the reduction in circulating sugar at the beginning of pregnancy.

As with the regulation of blood pressure, conflict about blood glucose involves potentially dangerous side effects: Insulin resistance during pregnancy increases the mother's risk of developing diabetes later in life (Feig, Zinman, Wang, & Hux, 2008), and when blood glucose levels are elevated for long periods, the mother may contract gestational diabetes mellitus (GDM)—a condition occurring in 7% of pregnancies in developed countries (American Diabetes Association, 2004). Mothers with GDM have larger babies than healthy mothers, supporting the theory that insulin resistance is a means for the fetus to obtain resources from the mother (Langer et al., 2005). The effects of prenatal conflict can have long-lasting consequences on metabolism and health: Maternal GDM in pregnancy increases the newborn's risk of developing insulin resistance and obesity in childhood (Boney, Verma, Tucker, & Vohr, 2005). Women over 35 years of age are at high risk for GDM (Ross, 2006). It could be hypothesized that

older women are shifting their threshold for parental investment, allowing current offspring to get more resources in view of their decreasing fertility.

Pregnancy Sickness

Pregnancy sickness or nausea and vomiting of pregnancy (NVP) is a common pattern of food aversion, nausea, and vomiting experienced by most women during the first trimester of pregnancy. NVP peaks around Weeks 9–14 and typically ends by the fourth month of gestation. From the evolutionary point of view, there is strong support for the hypothesis that NVP has the adaptive function of protecting the fetus from ingestion of toxins and teratogens during the most sensitive phase of organogenesis (Profet, 1992); in addition, Flaxman and Sherman (2000) proposed that the especially strong aversion for meat, fish, poultry, and eggs displayed by pregnant women is designed to protect both the developing fetus and the mother (who undergoes physiological immunosuppression during pregnancy) from food-borne pathogens such as bacteria and fungi. Consistent with this hypothesis, stronger NVP symptoms are associated with better pregnancy outcomes, such as lowered risk of miscarriage and still-birth (reviewed in Flaxman & Sherman, 2000; Forbes, 2002); moreover, dietary differences across countries correlate with the prevalence of NVP in a way consistent with the protection hypothesis (Pepper & Roberts, 2006).

The protection hypothesis was challenged by Forbes (2002), who put forth the alternative evolutionary hypothesis that NVP is a nonadaptive outcome of maternal–fetal conflict. The most likely endocrine basis for NVP is the placental hormone human chorionic gonadotropin (hCG), which is abundantly produced by the embryo during the first trimester. The primary function of hCG is to maintain pregnancy by preventing degeneration of the corpus luteum, and there is consistent evidence that it behaves as a “honest signal” of fetal vigor and genetic quality (e.g., absence of chromosomal abnormalities; Forbes, 1997, 2002). Forbes argued that viable fetuses produce higher hCG levels and, incidentally, higher NVP symptoms in mothers; thus, the observed relation between NVP severity and good pregnancy outcomes could be due to higher fetal quality and not to the protective effects of NVP. The conflict hypothesis would also explain why extremely strong NVP (known as *hyperemesis gravidarum*) can be highly debilitating for the mother and sometimes fatal for both mother and fetus (e.g., Abell & Riely, 1992). If the intensity of NVP is the outcome of a conflict between mother and fetus, the mother may sometimes end up suffering a cost that is beyond her own optimum. Further, the conflict can occasionally escalate and get out of hand, killing one or both parties as an unintended side effect.

Whereas the two hypotheses are presented and discussed as mutually exclusive (e.g., Flaxman & Sherman, 2008), they are probably compatible at a deeper level: The key is to consider NVP as a form of parental investment, with protective benefits for the fetus and nutritional costs for the mother (Del Giudice, 2007). POCT then predicts that the optimal severity of NVP should differ when viewed from the perspective of the mother and that of the fetus, with the fetus benefiting more from severe symptoms than the mother. In this perspective, NVP would be an adaptation, but a costly one, especially for the mother. Although hCG could have evolved as a signal of viability, it may have taken on an additional

role as a regulator of maternal investment during pregnancy. This hypothesis is consistent with the paternally biased expression of hCG, because paternally expressed genes often evolve so as to increase the level of maternal investment (see the Conflict Over Mate Choice section).

Future Directions

The range of potential conflicts between mothers and fetuses extends beyond nutrition and growth. One important arena of conflict that has been relatively neglected is that of spontaneous abortion. Spontaneous abortion in the first trimester often occurs because of genetic or chromosomal anomalies in the embryo (Forbes, 2002). Because pregnancy involves high physiological costs for the mother, spontaneous abortion is regulated by mechanisms that interrupt pregnancy if fetal quality falls under a certain threshold, before substantial investment is made (see Forbes, 1997). As with every type of maternal investment, the genetic interests of the mother and the fetus can be expected to diverge about the optimal threshold for abortion; specifically, the mother should implement a more stringent filter than is optimal from the perspective of the fetus. Importantly, maternal stress has been shown to increase the likelihood of miscarriage (e.g., Arck et al., 2001; Nepomnaschy et al., 2006); thus, the conflict outcome appears to be partly regulated by the psychobiological state of the mother (see Figure 1: “parental condition/resources” → “parental investment”).

Another puzzling phenomenon that might be illuminated by a POC perspective is that of so-called “denied pregnancy” or, more aptly, “cryptic pregnancy” (Del Giudice, 2007). A startling number of human pregnancies go unrecognized by the mother and her relatives until the end of the second trimester (about 1 pregnancy in 475), and in some cases until delivery (about 1 in 2,500; Wessel, Endrikat, & Büscher, 2002). This phenomenon has been traditionally interpreted in a psychodynamic framework, as involving psychotic-like defenses against deeply conflictual unconscious feelings. However, women experiencing cryptic pregnancy typically lack NVP symptoms, may show pseudomenstrual bleedings, report reduced abdominal swelling, and often deliver underweight babies (reviewed in Del Giudice, 2007). Del Giudice (2007) argued that this constellation of features reflects an unusually low level of maternal investment and can mislead women into believing they are not pregnant; intriguingly, both NVP and menstruation cessation are likely regulated by fetal hCG, suggesting a key role of this hormone in the etiology of cryptic pregnancy. At the functional level, Del Giudice proposed three explanatory hypotheses for the occurrence of cryptic pregnancy: This condition may arise as a nonadaptive by-product of mother–fetus conflict; as a result of low fetal quality, when hCG levels are just above the abortion threshold; and as an “emergency strategy” triggered by social stressors—a strategy aimed at reducing investment to maximize the likelihood of successful delivery in a threatening environment. Future research on this fascinating topic could afford new insight into the mechanisms that regulate the allocation of maternal investment during pregnancy and, most importantly, the role played by psychological and social factors.

Finally, framing human pregnancy in the perspective of POC will help researchers generate new hypotheses on how social and ecological factors may affect important outcomes such as sponta-

neous abortions, pregnancy sickness, hypertension, diabetes, and high/low birth weight. For example, a comparative study by Long (2005) showed that fetal development is faster in primate species with more promiscuous mating systems compared with monogamous species, even controlling for phylogenetic confounds. Moreover, fetal growth is fastest in species where the fetus (by virtue of placental structure) has more direct access to maternal nutrients. These data are consistent with battleground models (see above) that predict a higher level of POC in mating systems where interdependence between mothers and fathers is low. Cross-cultural variation in human mating systems (or even variation in individual reproductive strategies) might be associated with more or less intense mother–fetus conflict and, consequently, with differences in the incidence of pregnancy-related outcomes such as NVP, hypertension, and low birth weight. Even more detailed predictions could be made by applying conflict resolution models to human pregnancy. Unfortunately, current data do not permit precise characterization of the effect of supply on demand functions involved in mother–fetal exchanges; for this reason, the quantitative description of how mother and fetus respond to each other during pregnancy would be a valuable topic for future research, ripe with potential clinical implications.

Weaning Conflict

After birth, the primary focus of mother–child conflict shifts to the intensity and duration of breast-feeding. Beyond direct nutritional benefits, breast-feeding in human mothers confers health benefits to their children (Cunningham, Jelliffe, & Jelliffe, 1991; McDade & Worthman, 1998), including reduced risk of gastrointestinal infections, respiratory infections, middle ear infections, meningitis, and immune system disorders in infants. The decision to breast-feed, including the duration of breast-feeding and the timing of weaning, therefore has significant relevance to the health of the child. To provide a foundation for understanding weaning conflict in humans, we first describe weaning in other mammals and primates, articulating the principles that underlie weaning conflict in general, and then we apply these principles to understanding weaning conflict in humans.

Weaning Conflict in Primates and Other Mammals

Conflict during weaning in mammals has been well studied and is considered the prototypical case of parent–child conflict over a limited resource (Fouts et al., 2005). Trivers (1974) used the case of mammalian weaning to illustrate the key principles of POCT. According to POCT, parents and their children are expected to disagree over the duration of nursing. Because resources invested in breast-feeding cannot be used for future reproduction, the optimal duration of nursing should differ from the perspectives of parents and children, with children selected to seek a longer duration of breast-feeding than mothers are selected to provide. Although it is in the interests of both mothers and children to achieve some balance between maternal investment in current versus future offspring, the optimal tipping point—that is, when to shift investment away from current offspring—can differ sharply for mothers and offspring (see The Logic of POCT section).

Some controversy surrounds weaning conflict in primates, as studies have often produced conflicting findings (for an extensive

review of the debate, see Maestriperi, 2002). As a result, the POCT interpretation of conflict between primate infants and their mothers has been challenged in the literature. For example, Altmann (1980) proposed a *timing hypothesis* whereby weaning conflict is not a product of differences in optimal investment between infant and mother but rather a conditioning process by which infants are trained when to and when not to solicit access to the mother's nipple. Other challenges to POCT within the primate literature include the observation that conflict occurs at times other than weaning, that offspring may wean themselves without maternal interjection, and that infant solicitation appears to track maternal condition and ecological conditions (e.g., Barrett & Henzi, 2000; Bateson, 1994). In his extensive review of the literature, including the main challenges to POCT, Maestriperi (2002) concludes that these arguments against POCT stem primarily from differences in interpretation of data as well as from the incorrect assumption that only genetic relatedness contributes to differences in optimal parental investment between parent and offspring.

Despite the continued debate regarding POCT and primate weaning conflict, converging lines of evidence in primates show that the weaning process typically coincides with maternal resumption of mating (Maestriperi, 2002). A prediction of POCT is that weaning conflict should increase around transition points when mothers reallocate investment away from nursing and toward the production of new offspring. It is at such transition points when competition between current and future offspring is most salient. A well-established phenomena in the primate literature on weaning is the tendency for nipple solicitation to increase markedly when their mothers resume estrus (i.e., fertile ovulatory cycles). This tendency has been shown in several primate species, including gold howler monkeys (*Alouatta caraya*; Pavé, Kowalewski, Paker, & Zunino, 2010), rhesus macaques (*Macaca mulatta*; Berman, Rasmussen, & Suomi, 1993; Gomendio, 1991), and white-headed langurs (*Trachypithecus leucocephalus*; Zhao, Tan, & Pan, 2008).

One study in particular (Gomendio, 1991) compared rhesus mothers who did and did not conceive during the next breeding season and found that the offspring of nonconceiving mothers were more successful in their attempts to gain access to the nipple. Studies of nursing have shown that the energetic stress of lactation reduces fertility by suppressing the activity of the hypothalamic-pituitary-ovarian axis (e.g., Ellison, 2001). The increase in breast-feeding attempts by offspring that coincides with estrus, therefore, may function to delay or prevent the mothers from reproducing. Significant differences were also found between conceiving and nonconceiving mothers in their rates of rejecting nursing offspring: Conceiving mothers rebuffed their infant's nursing attempts more often than did nonconceiving mothers. Nonetheless, no differences were found in begging intensity between offspring of conceiving and nonconceiving mothers during estrus (Gomendio, 1991). Gomendio interpreted these data as a challenge to POCT, because differences between conceivers and nonconceivers were the result of maternal rather than infant behavior. However, as noted by Maestriperi (2002), this finding does not necessarily challenge POCT, as it concerns the way conflict is resolved rather than its ultimate cause. As discussed in The Logic of POCT section, conflict can be resolved in a range of different ways, and supply/demand mechanisms play a crucial role in conflict resolution. The data by Gomendio (1991) suggest that the resolution of weaning

conflict and the attendant likelihood of future conception was mediated by maternal behavior (i.e., mothers maintained control over allocation of investment); although infants engaged in tactics to solicit additional investment from mothers, additional investment did not appear to affect solicitation. This is evidence of a flat slope of the effect of supply on demand, a pattern that should lead to conflict resolution at the parental optimum (see *The Logic of POCT* section).

Finally, offspring solicitation/demand for parental investment as well as associated levels of parent–child conflict depend on resource availability, with conflict decreasing as a function of greater availability of weaning foods (see the *Determinants of Parental Investment and Offspring Demand* section). Among chacma baboons, for example, infants only have tantrums during weaning when alternative forms of food are unavailable; these tantrums are followed by an increase in the amount of investment received from the mothers (Barrett & Henzi, 2000).

Weaning Conflict in Humans

Humans are extremely unusual in the animal world in raising multiple dependent offspring of different ages. Offspring in almost all other species need to be able to feed themselves after they are weaned, as parents generally do not provision older offspring after they have produced new offspring. Humans neither bear and raise only one offspring at a time (as the other great apes do, creating “pure” inter-brood competition) nor produce litters (as many other mammalian species do, generating “pure” intra-brood competition). The battleground of weaning conflict in humans, therefore, does not conform to a strictly inter-brood or intra-brood model. Because humans generally do not produce litters, multiple births excepted (though in hunter-gatherer societies, only one twin usually is raised and the other sacrificed; Daly & Wilson, 1984, 1988), the degree of intra-brood competition over mother’s milk is essentially zero. Nonetheless, nursing may still be a focus of sibling competition because it takes considerable time and energy away from the mother—time and energy that could have been devoted to older siblings. For example, one reported barrier to infant breastfeeding is maternal workload, including caring for other children (Ahluwalia, Morrow, & Hsia, 2005; Ogbuanu et al., 2009). This barrier suggests that mothers may make trade-offs in their time allocation, devoting energy and resources to either nursing or caring for their older children. In general, the time and resources of mothers, of which energetic expenditures on nursing is one component, should be a central point of contention among siblings.

Because potential conflicts over weaning in modern societies are mitigated by the widespread availability of alternative food sources for infants (e.g., formula, mashed baby foods), traditional societies—where decisions over duration of lactation present mothers with real energetic and reproductive trade-offs—provide a more valid context for studying weaning conflict. Anthropological data on weaning processes in such societies are abundant and provide a solid basis for testing the main predictions of POCT. The most detailed data come from a series of studies on the weaning patterns of Bofi foragers and farmers of Central Africa. The Bofi foragers are a patrilocal group that hunt primarily with nets and subsist on small to medium sized game together with plant foods and insects gathered from the local environment. Bofi farmers are

slash-and-burn horticulturalists. Both the foragers and farmers are largely monogamous.

Fouts and colleagues (Fouts, 2004; Fouts et al., 2005) found that, in both the farmers and foragers, conflict between parent and child was initially low postpartum but gradually increased over time as nursing frequency was reduced and the weaning process began (see also Pryce, 1995). Farmer children were weaned at earlier ages than foraging children, and this may partly explain why they displayed more weaning distress (Fouts et al., 2005). In addition to child age, low overall levels of nursing and the mother becoming pregnant each predicted increased levels of fussing and crying by children during nursing/weaning. Each of these factors influences or reflects the amount of investment that mothers allocate toward offspring and, therefore, contributes to parent–child conflict. For example, pregnancy usually coincides with a decrease in nursing. Among the Bofi, pregnancy was most strongly associated with fussiness and crying when weaning was abrupt rather than gradual.

The tendency for weaning to occur at pregnancy is not unique to the Bofi; cross-culturally, pregnancy is a common reason for initiating weaning (McDade & Worthman, 1998). For example, among the !Kung, weaning typically occurs when the mother becomes pregnant (Konner, 2005) and is completed well before the birth of the new child. Likewise, among the Turkana pastoralists of Kenya, conflict tends to be high when mothers resume sexual relations with their husbands. Resumption of sexual relations represents a transition point where reproductive effort is being diverted away from parental investment and toward mating effort. Indeed, the most frequently cited reason for weaning among the Turkana was pregnancy (Gray, 1996). Thus, consistent with POCT, conflict between human mothers and their children appears to track maternal resource allocation decisions between investment in current versus future offspring.

Control of investment (e.g., nursing) in nonindustrial societies generally lies in the hands of the mother. Weaning practices among the Bofi and Turkana, for example, involve the application of substances to the mother’s nipples to discourage nursing (e.g., Fouts et al., 2005; Gray, 1996). An additional tactic used by the Turkana is to simply leave the child in the care of alloparents for durations from a few hours to a few days, with the mother often leaving the camp entirely. Although the effect of supply on demand was not measured among the Turkana, evidence from the Bofi and from the Karo Batak of Indonesia (Kushnick, 2009) suggests that two effects of supply on demand mechanisms can occur. Among the Bofi, infant fussiness was greater when weaning was more abrupt, suggesting that reduction in supply leads to increased demand. Among the Karo Batak, however, a positive relationship was found between provisioning and infant fussiness, where longer periods of suckling were followed by longer periods of fussing. Thus, the effect of supply on demand associated with human lactation may show a complex pattern and may possibly change depending on the phase of weaning.

Finally, ecological and social contexts influence the timing of weaning and subsequent parent–child conflict. The availability of non-breast-milk foods and their cost, maternal workload, social support, and ideology are all related to weaning in preindustrial societies (McDade & Worthman, 1998). In total, socioecological factors such as workload and social support influence the benefit–

cost ratio of nursing from the mother's perspective and, through it, weaning processes and parent–child conflict.

Future Directions

An important avenue for future research will be applying POCT to predict individual and cultural variation in the initiation and termination of weaning. Nursing can be highly valuable to infants but, at the same time, has the potential to become highly stressful for both mother and child. It is then important to understand the factors that contribute to variation in nursing behavior (Pickler, 2009). To be certain, applying discoveries about weaning conflict in preindustrial societies to industrial societies may be complicated. For example, nearly all mothers in preindustrial societies breast-feed their newborn infants to some degree, due at least in part to the lack of alternatives food sources. In industrial societies, however, formula has been marketed as a viable alternative to breast-feeding, and up to 60% of women do not breast-feed at all (Ogbuanu et al., 2009). Nonetheless, we suggest that some of the same factors that influence the timing of weaning in traditional societies can be fruitfully studied in industrial societies as well. For example, several studies have shown that maternal workload (such as household responsibilities) and caring for other children are predictive of maternal decisions to breast-feed (e.g., Ahluwalia et al., 2005; Guttman & Zimmerman, 2000; Ogbuanu et al., 2009). In a POCT perspective, these factors influence the costs of nursing and shift mothers' allocation decisions between different facets of life history strategies. Thus, applying POCT to this research field can prompt researchers to ask novel questions about the decision to breast-feed. For example, how does the need and fitness of extant children contribute to the decision to breast-feed a new infant?

Genetic Relatedness and Family Conflict

Although weaning can be a time of stress and conflict, human children (unlike many other primates) remain dependent on their parents for many years after their mother stops breast-feeding them. Indeed, parents and other family members fully provide for children at least until the beginning of middle childhood (see Bogin, 1997; Del Giudice, Angeleri, & Manera, 2009), and parental investment often continues through adolescence and early adulthood. During childhood, conflict over parental investment takes new forms, extending beyond the dyadic relationship with the mother, and ultimately involves all the members of the family—including siblings. This is why genetic relatedness becomes a major influence on the intensity and resolution of parent–child conflict. Despite the importance of relatedness, very few studies have used POCT as a framework to investigate its effects in human families (though see Schlomer et al., 2010). This is a very promising area of research, and one where major discoveries are probably waiting to be made.

Step-Families

Generally speaking, conflict between family members should be negatively associated with genetic relatedness. Lower genetic relatedness is predicted to increase conflict, and the most dramatic example (though not one directly derived from POCT) is provided by research on step-families. Qualitative differences in the parent–

child relationship can be drawn along lines of biological relatedness. For example, parents tend to be more warm and engage in more caretaking toward their biological children compared with step-children (Hetherington et al., 1999; O'Connor, Dunn, Jenkins, & Rasbash, 2006). Indeed, in a comprehensive study of adolescent family relationships, in step-families, Hetherington et al. (1999) reported that

A notable finding relating to parent–adolescent relationships in this study was the relative lack of differences in parenting related to being in a step-family or a non-step-family. Instead, biological relatedness between parent and adolescent was stronger in determining differences in parenting than family type. (p. 83)

Low genetic relatedness between adults and children in the family is associated not only with colder and less involved parenting but also with a higher probability of neglect, abuse, and homicide toward children. A consistent finding in the child abuse literature is that children in step-parent families are at considerably greater risk for neglect and abuse compared with families with two biological parents (e.g., Daly & Wilson, 1988, 2007; Wilson, Daly, & Weghorst, 1980). Although Daly and Wilson's work has generated intense controversy (e.g., Buller, 2005; Malkin & Lamb, 1994; Temrin, Buchmayer, & Enquist, 2000; Temrin, Nordlund, Rying, & Tullberg, 2011), they have (in our opinion) convincingly responded to criticism, often finding the predicted effect of step-parenting in their critics' own data (see Daly & Wilson, 2005, 2007). In addition, young children who live with at least one nonbiological parent (e.g., step, adopted, etc.) are at greater risk for fatal injury (Schnitzer & Ewigman, 2005), regardless of the injury being intentional or not (Tooley, Karakis, Stokes, & Ozanne-Smith, 2006). In total, these data indicate that low genetic relatedness is associated with elevated levels of conflict among family members, although other factors (e.g., higher disposition toward crime and violence in men who end up becoming step-fathers; Temrin et al., 2011) may plausibly contribute to the observed pattern of results.

Sibling Competition

Sibling competition is another domain in which genetic relatedness should substantially affect behavior. From an evolutionary perspective, competition between siblings functions to attain a disproportionate share of investment from parents, and offspring that are better competitors are able to secure more resources. This pattern of sibling rivalry is expected to emerge most strongly under conditions of resource scarcity (see the Determinants of Parental Investment and Offspring Demand section). Because sibling competition is often a zero-sum game, garnering of additional parental resources by more dominant siblings typically results in diminished resources for other siblings. Factors such as sibling number, individual offspring's competitive ability, parental condition and resources, and offspring need influence parental investment in current offspring (see Figure 1) and, through it, the degree of competition between siblings and its outcomes.

As discussed in The Logic of POCT section, in the context of intra-brood competition, greater sibling relatedness can be expected to (a) reduce the intensity of POC and (b) reduce competition between siblings for parental investment. The basis of these predictions is that convergence versus divergence of sibling inter-

ests and parent and offspring optima ultimately depends on genetic similarity. Consistent with this theorizing, Pollet (2007) reported that adult half siblings showed less social investment in one another (concern for the other, face to face contact) than did full siblings. In this study, maternal half siblings, who were also likely to be raised together, showed more social investment compared with paternal half siblings, suggesting that both co-residence while growing up and genetic relatedness influence sibling relationships. Another study by Smith (2007) found that monozygotic twins reported more sympathy and compassion and less rivalry, avoidance, and aggression with each other than did dizygotic twins. This result suggests that siblings may possess some (likely unconscious) mechanism allowing them to estimate the genetic relatedness with one another, possibly based on the degree of physical and/or psychological similarity. Finally, in another study conducted in a Mormon polygynist community, sibling solidarity was higher between full biological siblings than half siblings (Jankowiak & Diderich, 2000). This finding was particularly compelling because of the prolonged co-residence of half siblings and the ethos of the community, whose members intentionally sought to downplay genetic differences between children.

More recently, Schlomer et al. (2010) tested the hypothesis that reduced genetic relatedness between siblings would increase conflictual relationships between mothers and their adolescent children. In their study, levels of mother–child conflict were compared between families with and without a half sibling. Children who co-resided with a younger half sibling reported higher levels of conflict with their mothers compared with children without a younger half sibling. This effect persisted net of several family-level control variables, including socioeconomic status, number of co-residing children, parental divorce, and presence of a step-father. Although these results must be considered tentative pending replication, this is the first human research to document a phenomenon, clearly predicted by POCT, that has been previously demonstrated in cross-species comparisons of birds (Briskie et al., 1994): that decreasing offspring relatedness increases offspring solicitation/demand for parental investment.

Future Directions

There is still a lot to learn about the effects of relatedness on family conflict. POCT could be fruitfully adopted by developmental researchers, both as a tool to generate new predictions and as a general framework for interpreting and connecting the empirical findings. Although the effects of sibling relatedness have been investigated in a number of recent studies (see above), it is still unknown how children estimate relatedness and what cues they use. Potentially, relatedness cues could come from parents' behavior as well as from other, less explicit sources such as physical similarity and olfactory cues. These factors have been shown to influence fathers' behavior toward their children (e.g., Apicella & Marlowe, 2004, 2007; Burch & Gallup, 2000; Volk & Quinsey, 2007) but may be just as relevant to sibling relationships. Lastly, although studies of genetic relatedness between siblings suggest that half-sibling relationships are less cohesive than full sibling relationships, there is dearth of research trying to unpack the processes underlying these relationships. For example, much research has been conducted regarding sibling rivalry (e.g., Buhrmester, 1992; Buhrmester & Furman, 1990; Cicicille, 1995; Dunn,

Slomkowski, & Beardsall, 1994); however, POCT is not about rivalry *per se* but rather about competition for parental investment. So, in addition to overt rivalry, half-siblings may compete more for parental attention as well as being more sensitive to asymmetries in investment and parental favoritism.

Although relatedness between siblings should mainly affect intra-brood competition (see The Logic of POCT section), competition between present and future siblings (inter-brood) is expected to depend on the interdependence between parents. However, this parameter has been so far neglected in POCT-inspired research. Many interesting research questions may arise from consideration of parent interdependence—both at the level of cultural or social groups (e.g., how do different mating systems and/or different levels of partner availability affect parent–child conflict?) and at the level of individual families—including the following: Do parents adjust their behavior according to their perceived interdependence? Do children make (conscious or unconscious) estimates of the interdependence between their own parents, and if so, what cues do they use to that end? Does overt conflict between parents modulate parent–child conflict by providing children with cues of low interdependence?

Conflict Over Mate Choice

Among hunter-gatherers, and even more so in agricultural and pastoral societies, parents play an important role in choosing marriage partners for their children (Apostolou, 2010; Buunk et al., 2008). In many preindustrial societies, marriages are directly arranged by parents. However, even where arranged marriages are not the norm, it is often the case that children must gain their parents' approval before they are allowed to wed (Apostolou, 2007b, 2010). This suggests that parental influence on their children's mate choice has long been part of the evolutionary history of our species. Of course, the parents weighing in on children's mating decisions can generate intense conflict when parents and children disagree about the desirability of a potential mate. POCT helps explain why family conflict over mate choice is widespread and why disagreements tend to concentrate on some specific traits and qualities, such as physical attractiveness, dependability, and family background. From the vantage point of POCT, it is possible to understand the strategic reasons underlying parents' and children's preferences and to make predictions as to whether parents or children will favor a given characteristic over another.

As noted already by Trivers (1974), conflict over mate choice can be expected to arise whenever the characteristics of potential mates result in asymmetric costs and benefits for parents and children (see The Logic of POCT section). Why should this ever be the case? From a biological point of view, the benefits provided by a mate can be grouped into two main clusters. On the one hand, there is genetic quality (lack of deleterious mutations), indexed by traits such as health, beauty, athleticism, intelligence, and creativity (Miller, 2000; Thornhill & Gangestad, 1993; Thornhill & Møller, 1997). Higher genetic quality in a partner results (on average) in healthier, more successful, and more attractive offspring. On the other hand, a mate can bring benefits in terms of parental investment, either by directly caring for his/her offspring or by providing food, protection, wealth, and other resources. The potential for investment, in turn, depends both on the ability to invest (e.g., on the posses-

sion of sufficient resources and/or the ability to gain and defend them) and on the willingness to use one's resources to increase the welfare of family members. The latter is indexed by traits such as generosity, cooperativeness, affection toward children, and so on. Finally, the opportunity for beneficial political alliances between families constitutes an additional source of benefits to be gained through marriage. Note that health reflects genetic quality but at the same time contributes to the ability to provide for one's offspring. Likewise, a good family background can provide political benefits but also access to resources and wealth.

Genetic quality, investment potential, and political opportunities contribute in different ways to the fitness of parents and children, thus creating the conditions for POC to occur. Consider, for example, parent P with three offspring: A, B, and C. High genetic quality in A's partner contributes to parent P's fitness only through the genetic quality of A's own children (i.e., P's grandchildren through A). In contrast, the benefits coming from investment, cooperation, and political alliances can be shared to some extent by other family members (e.g., children B and C and their own children). Moreover, if A's partner is not an adequate provider, A's relatives (P, B, and C) will likely need to compensate by spending time and resources; this will inevitably limit their ability to invest in their own children and grandchildren. For all these reasons, when evaluating the suitability of a potential mate for A, B, or C, the parents, relative to the offspring themselves, should place more value on the ability to provide parental investment, the willingness to cooperate and invest, and the opportunity for political alliances and should place less value on attractiveness and other cues of genetic quality (Apostolou, 2007b; Buunk et al., 2008). Of course, genetic quality *does* benefit parents as well, so that parents' and offspring's preferred characteristics should be highly correlated. What is expected to differ between parents and children is the *relative* weighting of some characteristics; disagreements will be especially strong when a trade-off is involved—for example, when a potential mate is witty and good-looking but lazy, undependable, or born in a low-status family.

These predictions have received initial support in a series of recent empirical investigations. When asked about potential partners for their children, parents give more weight to investment potential, cooperation, and family background, and less weight to attractiveness and other cues of genetic quality, than when they are asked about a potential partner for themselves (Apostolou, 2007a, 2008a, 2008b). The data suggest that people are more willing to trade-off physical attractiveness when selecting a partner for their children compared with a partner for themselves. A similar pattern emerged when young adults from several different countries were asked to compare their own preferences with those of their parents by rating different traits as more or less unacceptable in a potential mate (Buunk et al., 2008; Buunk & Solano, 2010). Parental preferences for characteristics in an in-law are also moderated by the gender of the in-law. For example, in the case of a son-in-law, parents prefer characteristics such as industry, ambition, education, intelligence, and financial prospects more so than for a daughter-in-law. Conversely, preferred characteristics of a daughter-in-law

include housekeeping, cooking, chastity, and attractiveness (Apostolou, 2007a, 2008a).

Future Directions

The extension of POCT to family conflict about mating decisions is an exciting development, and one that will likely yield a rich empirical harvest over the coming years. This emerging theory and data illustrate that POC is not limited to pregnancy, infancy, and childhood but persists in different forms well into adulthood. At the same time, extant research in this area has important limitations. All studies have been based on reports by only one individual, and ratings are obtained based on hypothetical scenarios. Additional research is needed to independently compare the preferences of children and their parents, to examine the characteristics of actual long-term mates, and to study actual occurrences of family conflict over mate choice. Furthermore, parental preference for family background and social status is based on the logic that parents can use social and material resources gained from their child's marriage to enhance their own inclusive fitness. Differences in preferences may be observed when investment in other closely related individuals cannot impact their fitness, such as in dangerous and unpredictable environments (Ellis et al., 2009). Finally, future studies could explore how conflict is played out in actual behavior: What tactics do parents employ to influence their children's mating decisions? What counter-tactics do children adopt to limit parental influence? How do different cultural and social arrangements affect the range of options available to the various family members?

Genomic Imprinting

So far, we have discussed how the logic of POCT has been applied to individuals such as mothers, offspring, and siblings. David Haig (1997) was the first to realize that conflicts about parental investment can arise not only between parents and offspring but also between *different genes* within the same offspring—specifically, between genes inherited from the mother and genes inherited from the father. This form of intragenomic conflict (i.e., conflict between different genes in the same individual's genome) is tied to the phenomenon of genomic imprinting, and its evolutionary implications are spelled out in the *kinship theory* of imprinting developed by 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, that is, on whether it was contained in an ovum or a sperm. For example, the insulin-like growth Factor II gene (*IGF2*; coding an important growth factor; see below) is paternally expressed in humans, and its homologues are paternally expressed in various mammals including rats, mice, and sheep (see Haig, 2004). 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, usually by DNA methylation and histone modifica-

tion; 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. Furthermore, gene silencing needs not follow an all-or-none pattern; in many instances, the expression of the maternal and paternal copy of an imprinted gene may only differ in degree (see Schalkwyk et al., 2010). To date, imprinted genes have been found only in mammals and angiosperm plants. By typical estimates, less than 1% of the mammalian genome is imprinted (see Bartolomei & Tilghman, 1997; Wilkins, 2008); however, newer data suggest that parent-of-origin effects on methylation patterns may involve as much as 1.5% of human genes (Schalkwyk et al., 2010), and a study of genetic expression in the mouse brain indicated that more than 5% of brain-expressed genes may be imprinted (Gregg et al., 2010; see also Kelsey, 2011).

Let us consider POC from the perspective of imprinted genes. A maternally derived allele in the offspring has a 50% probability of ending up in a future sibling. However, if there is any degree of multiple paternity, the same probability for a paternally derived allele 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 nonimprinted autosomal genes, this hardly matters because they carry no information whatsoever about their parent of origin. For imprinted genes, however, this phenomenon has remarkable implications: Because a paternally expressed gene is (on average) less strongly related to future siblings than its maternally expressed counterparts, it can be expected to discount the well-being of future siblings at the benefit of the individual offspring. Thus, paternally expressed genes are expected to “side” with the offspring in the regulation of maternal investment and to evolve so as to increase the transfer of maternal resources to the offspring (e.g., by increasing its fetal growth rate). Maternally expressed genes are expected to evolve in the opposite direction, thus inhibiting the transfer of maternal resources to the offspring. 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 (which are exceedingly rare).² Note that the kinship theory is not the only hypothesis about the evolution of genomic imprinting; alternative models have been put forth in the literature (e.g., Beaudet & Jiang, 2002; for a review, see Wilkins & Haig, 2003).

In its original formulation, the kinship theory of imprinting was essentially concerned with inter-brood sibling competition. Haig and Wilkins (2000) extended the model to cover intra-brood competition. They showed that paternally expressed genes should increase offspring solicitation/demand for parental investment if increased demand reduces the amount of resources to be divided between siblings but increases the share received by those offspring that are more demanding. In contrast, maternally expressed genes should evolve in the opposite direction and should tend to reduce offspring solicitation/demand for parental investment if this reduction causes all siblings to be better off. 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 severity of sibling competition for parental investment. On the contrary, maternally expressed genes should become

“resource inhibitors” and should reduce the individual offspring’s demands to favor siblings as a group. The tug-of-war between maternally and paternally imprinted genes is expected to lead to costly manifestations of conflict, either at the physiological or behavioral level.

Although the kinship theory of imprinting can be easily applied to POC, its scope is not limited to interactions with parents and siblings; indeed, the effects of asymmetric relatedness potentially extend to any interaction with patrilineal versus matrilineal kin (e.g., to relations with paternal vs. maternal grandparents). For example, in a species where males disperse and juveniles live together with their matrilineal (female) relatives until maturity, maternal genes can be expected to evolve as to favor highly cooperative and altruistic behaviors in juveniles. To date, however, most empirical applications have focused on mother–offspring interactions and, in particular, with the conflicts involved in the regulation of maternal investment during pregnancy.

Imprinted Genes and Prenatal Conflicts

In the previous section, we reviewed some of the mechanisms involved in maternal–fetal conflict over investment and discussed how the fetus can attempt to manipulate maternal physiology to increase resource transfer beyond the maternal optimum. Not surprisingly, many imprinted genes are critically involved in the regulation of fetal growth. In humans, *IGF2* is paternally expressed and promotes fetal growth; *IGF2* overexpression results in overgrowth symptoms and is associated with the Beckwith–Wiedemann syndrome, a pathological condition involving prenatal overgrowth and enlarged placenta. Another gene, *H19*, is maternally expressed and has opposite growth-inhibitory effects. *H19* produces a noncoding RNA that apparently acts by suppressing *IGF2* expression, thus providing an example of direct antagonism between a paternally and a maternally expressed gene. In mice (but not in humans), the IGF-II receptor gene (*Igf2r*) is maternally expressed and behaves in a similarly antagonistic way: The IGF-II receptor promotes the degradation of paternally expressed IGF-II. Another growth-related gene in humans (and mice) is the maternally expressed *IPL*, which is highly expressed in the placenta and, if inactivated, results in placental overgrowth. Several other imprinted genes are expressed during fetal development, although their function (and their possible relationship to the kinship theory) is presently less clear (reviewed in Haig, 2004).

As discussed in the previous section, maternal hypertension and pre-eclampsia can sometimes be interpreted as the result of mother–fetus conflict over blood supply. A gene associated with pre-eclampsia, *STOX1*, has been suspected for some time to be imprinted and maternally expressed (e.g., Arngrímsson, 2005; Úbeda & Wilkins, 2008). Later analyses have cast doubts on the possibility that *STOX1* itself is imprinted, but *STOX1* is a transcription factor that regulates several other genes, at least one of

² For the purposes of the present article, we focus on the “weak” version of the kinship theory of imprinting, concerning the effects of selection on genes that (for whatever reason) show parent-specific expression. The “strong” version of the theory goes further and maintains that kinship relations actually *explain* the evolution of parent-specific expression, with imprinting evolving as an adaptive strategy in presence of asymmetric relatedness (see Haig, 2004).

which (*CTNNA3*) is known to be imprinted (see Oudejans & van Dijk, 2008). Thus, parent-specific expression may be involved in the physiological regulation of fetal blood supply.

Finally, placental hormones probably constitute the main channels for fetal manipulation (see above). Formal modeling by Haig (1996) indicates that if hormones can be used by the fetus as a way of manipulating maternal physiology, and if there is some degree of multiple paternity between successive offspring, we should sometimes expect fetal hormones to be produced (or up-regulated) by paternally expressed genes. This is especially true when species give birth to singletons (as humans typically do), so that all the relevant conflict is inter-brood, and the benefits of hormonal manipulation do not have to be shared with siblings. In addition, multiple paternity *within* litters should reduce fetal manipulation and render the evolution of paternally biased expression less likely. Although there is still little research on the imprinting status of placental hormones, there is indirect evidence that the gene coding for the β -subunit of hCG may be imprinted and paternally expressed (Goshen, Gonik, de Groot, & Hochberg, 1994) and that the hCG receptor on the maternal side may be imprinted too (Allen et al., 2003). These are important findings, given that hCG participates in several physiological pathways potentially related to prenatal conflict (e.g., spontaneous abortion, pregnancy sickness) and seems to act as a maximizer of maternal investment during pregnancy.

Genomic Imprinting After Birth

Although several imprinted genes are involved in fetal and placental development, many of them are active after birth, with a substantial subset being expressed in the brain (Davies, Isles, & Wilkinson, 2005; Gregg et al., 2010; Isles, Davies, & Wilkinson, 2006). This suggests that imprinted genes may continue to participate in the regulation of POC 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 (W. M. 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 GABA. Even more intriguingly, there are cues that imprinted genes may impact the oxytocin and vasopressin systems, which are crucially involved in the neurobiology of parent–child attachment and adult couple formation (Davies, Lynn, Relkovic, & Wilkinson, 2008).

At present, most of the empirical evidence for behavioral effects of imprinted genes in humans comes from the study of two imprinting-related syndromes caused by mutations or deletions on the long arm of chromosome 15: Angelman syndrome and Prader-Willi syndrome (PWS). These syndromes result from opposite patterns of genetic disruption and, as predicted by the kinship theory, show largely opposite phenotypes that relate to different levels of infant demand. Angelman syndrome (due to paternal overexpression and/or maternal underexpression) is associated with enhanced activity, prolonged suckling, bouts of laughter, and sleeping problems; on the contrary, PWS (due to maternal overexpression and/or paternal underexpression) includes reduced activity, poor suckling, undergrowth, weak crying, and sleepiness (all traits that reduce demands on the mother). In PWS, hunger

regulation changes dramatically after infancy, with PWS-affected children developing insatiable appetite and often becoming obese (see W. M. Brown & Consedine, 2004; Crespi & Badcock, 2008b; Haig & Warthon, 2003; Úbeda, 2008). A possible evolutionary explanation for this phenotypic 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). Another interpretation comes from the *generalized kinship theory* developed by Úbeda (2008), which extends the predictions of the kinship theory to mating systems where fathers provide parental investment in addition to mothers. In such species (humans included), the effects associated to imprinted genes can be expected to *reverse* after weaning, with paternally expressed genes reducing offspring demands and maternally expressed genes increasing them.

The psychological implications of imprinting could be even more wide-ranging than suggested by the above sketch. Recently, Crespi and Badcock (2008b; also see Badcock, 2009) argued that genomic imprinting can help explain the evolution of the human brain and the origin of some important psychological disorders. They reviewed a large body of evidence linking imprinted genes to the etiology of autism and psychosis, and they 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 to a “maternally biased” development. Although Crespi and Badcock's model is still speculative in several respects, and has been met with criticism by some researchers (e.g., Dickins, Dickins, & Dickins, 2008; Keller, 2008; Thakkar, Matthews, & Park, 2008; but see also Crespi & Badcock, 2008a; Crespi, Stead, & Elliot, 2010), it does hold considerable promise for an integrated evolutionary theory of psychopathology and may be useful to understand normal variation in personality as well (see Del Giudice, Angeleri, Brizio, & Elena, 2010). A better understanding of the genetic and epigenetic basis of autism and psychosis may also permit the development of improved methods for the early diagnosis and treatment of these conditions.

Future Directions

The idea that infant and child behavior is shaped by the action of imprinted genes opens up exciting avenues for research at the interface of developmental psychology, developmental neurobiology, and behavior genetics. First, understanding the mechanisms and function of imprinting will likely shed light on the genetic basis of POC and its regulation at the neural and physiological level. Second, the study of genomic imprinting could grant researchers a deeper understanding of the dynamics of gene–environment interactions in development (see Meaney, 2010). Genomic imprinting is a kind of epigenetic modification (i.e., a reversible modification that affects genetic expression without altering the DNA sequence); for this reason, imprinted genes can—in principle—evolve the ability to respond to environmental factors and could participate in the regulation of individual plasticity and in the inter-generational transmission of information about local environmental conditions. One can speculate that specific environmental and social cues (relating, e.g., to mating systems, resource levels, or parental conflict) might affect the im-

printing status of some genes during development, thus increasing or reducing the intensity of conflict between the paternal and maternal genome. At the same time, individual variation in the sequence of imprinted genes (and/or in the genes coding for the imprinting machinery) may shift the balance between maternal and paternal expression, thus contributing to the development of individual differences personality and social behavior.

Human family life is complex, and parental investment in our species can extend for very long periods of time (in the order of decades) and even through multiple generations. For this reason, it is reasonable to anticipate that imprinted genes will be found to be involved in a wide range of key areas of development, including parent–child attachment, adolescent conflict, and even the development of sexual and mating behavior (Del Giudice et al., 2010; Úbeda & Gardner, 2010). Haig (2010) recently proposed that imprinted genes could have been conspicuously involved in the evolution of several key features of human life history, such as early weaning and slow childhood growth. Clearly, the study of family conflict within the genome holds considerable promise for the future of developmental psychology and for its further integration with the biological sciences.

Conclusions

In this article, we introduced the biological theory of POC and reviewed several applications to family conflict, from prenatal conflict between mothers and fetuses to conflict over mate choice and marriage. Although these topics do not exhaust the potential range of applications, their breadth makes it apparent that POCT is indeed a powerful framework for the integrative study of family relationships. Moreover, as discussed in the Genomic Imprinting section, conflictual family dynamics at the behavioral and/or genetic level can have far-reaching implications for other areas of research, such as personality and psychopathology (e.g., Crespi & Badcock, 2008a; Del Giudice et al., 2010; Sulloway, 1996).

Although POCT is invaluable in the study of behavioral conflict (and conflict resolution), it is *not* a theory of behavioral conflict. Rather, POCT highlights the pervasive conflict of interest that exists between parents and offspring and the wide range of physiological, behavioral, and relational processes that have been shaped by this conflict over evolution. Furthermore, POCT should not be applied indiscriminately to *all* conflict within families. The domain of POCT is limited to behaviors that increase the fitness of offspring at the expense of their parents (or vice versa) and, in particular, to the allocation of parental investment among offspring.

Thus, the theory is not particularly informative about conflict over issues such as “what TV show will the family watch that night?” or “will Kayla take out the garbage?” Rather, returning to the hypothetical Knight family, the theory concerns conflict over issues that involve fitness trade-offs between children, such as “will Mr. Knight devote significant time and resources to developing Kayla’s sociocompetitive abilities, or will he put that effort into enhancing his own status to gain additional mating opportunities?”; “will Mrs. Knight quit her job to stay home and take care of Alicia, giving her the best start in life, even though the loss of income will undermine Ryan’s sociocompetitive status?”; and “will Ryan use his strength and first-born position in the family to monopolize scarce resources at the expense of his sisters?” Opti-

mal solutions to these kinds of resource allocation and competition problems differ from the perspectives of Mr. Knight, Mrs. Knight, Ryan, Kayla, and Alicia, and it is these differences that form the foundation of conflict, as predicted and explained by POCT and associated evolutionary models.

POCT has several features that make it especially attractive as a guide for psychological research. On the one hand, the main insights of POCT are relatively simple and straightforward (see The Logic of POCT section), and they can be used to derive novel, interesting predictions from the basic facts of human family structure and mating ecology. On the other hand, the details of conflict resolution depend on a complex network of causal effects taking place both within and outside the family (see the Determinants of Parental Investment and Offspring Demand section). Mapping those effects allows for finer grained modeling of specific processes (such as investment solicitation and sibling competition) and their realization in behavior, cognition, and physiology. The broader ecological dynamics captured by life history theory places POCT in a larger framework and makes the theory more applicable to real-life problems and situations. Finally, POCT extends smoothly from the level of behavior to that of physiology and genetic expression (see the Prenatal Conflict and Genomic Imprinting sections); for this reason, it can serve as an effective theoretical bridge between traditionally separate disciplines, such as developmental psychology, psychobiology, and behavior genetics.

Despite the promise of POCT as an integrative framework for developmental and family psychology, most of its applications are still in their infancy, even if they have already generated a remarkable number of testable hypotheses and empirical studies. In the following paragraphs, we summarize what we believe are the main opportunities and challenges for future research.

Opportunities and Challenges

Up to now, POCT has been applied to individual instances of family conflict, such as conflict over weaning or mate choice. An important task in the near future will be to fully integrate POCT into a comprehensive theory of development and parent–child relations. At present, attachment theory (see Cassidy & Shaver, 2008) is the mainstream approach in developmental psychology, and life history theory is emerging as the leading evolutionary framework for the study of human development (Ellis et al., 2009). The two approaches are not in competition; indeed, they share a common background in evolutionary biology, and attachment theory can be reformulated and extended from the broader perspective of life history theory (Belsky, Steinberg, & Draper, 1991; Chisholm, 1999; Del Giudice, 2009; Del Giudice & Belsky, 2010). Although researchers in this area have given some consideration to POC (e.g., Belsky, 1999; Del Giudice & Belsky, 2011b), there is still much work to be done to fully integrate POCT into this emerging framework. In the Determinants of Parental Investment and Offspring Demand section, we started to draw connections between life history theory and POCT by describing how ecological factors—such as unpredictability, resource abundance, and mate availability—modulate POC. However, a deeper integration between life history theory, attachment theory, and POCT will require more explicit modeling and more empirical data on the

mechanisms through which attachment relations modulate parental investment (see The Logic of POCT section).

This brings us to one of the main challenges in the application of POCT to human families. As discussed in The Logic of POCT section, going beyond the simple predictions afforded by battleground models comes at a price: the need to gather detailed empirical data on the mechanics of conflict resolution. For example, knowledge of the effect of supply on demand is required to determine the outcome of conflict in the formulation by Parker et al. (2002). Detailed empirical data on conflict resolution are also required to model the patterns of genetic coadaptation between parents' investment and children's demand, a fascinating topic of research at the frontier of behavior genetics (see Kölliker, Brodie, & Moore, 2005; Kölliker & Richner, 2001; Smiseth, Wright, & Kölliker, 2008). Fortunately, the more recent developments of POCT provide solid guidelines about the kind of data that researchers need to gather to benefit from the full predictive power of POC models. Once the data are in, we believe the field will also benefit from more extensive collaboration between psychologists and theoretical biologists so that quantitative models will integrate (and, in some cases, replace) the less precise verbal or semiquantitative models that currently predominate in evolutionary psychology.

In addition to making predictions on conflict intensity and resolution, POCT is extremely useful as a guide to generating novel hypotheses about the behavioral and physiological mechanisms that mediate family conflict. In the present article, we suggested several potential lines of research inspired by careful consideration of evolutionary conflict dynamics. For example, the interdependence between the mother's and the father's reproductive success is a key variable in POC models (alongside genetic relatedness), but it has received virtually no attention in the empirical literature. It is at least plausible to suggest that children may have evolved mechanisms that detect and encode information about parental interdependence, both in the local ecology and in their own family (see the Genetic Relatedness and Family Conflict section). Another fascinating (and neglected) topic of research is that of tactics and counter-tactics in the negotiation of mate choice and marriage (see the Conflict Over Mate Choice section). At the level of physiology, the mechanisms that mediate the effects of social stressors on fertility and spontaneous abortion may be better understood from a conflict perspective (see the Prenatal Conflict section; Del Giudice, 2007). However, it will be even more interesting to understand how parent–child conflict has shaped the genetic and neurobiological mechanisms underlying attachment relations (see the Genomic Imprinting section). Another crucial direction for future research is to ask new questions about the time course of family conflict: Do ecological factors alter the timing of conflict peaks? Do shifts in conflict type and intensity correspond to shifts in genetic expression, and what is the role played by imprinted genes? Finally, evolutionary models of developmental stages (e.g., Del Giudice & Belsky, 2011a) would be greatly enriched by a deeper integration with models of POC.

In conclusion, we believe that the time has come for psychology to embrace POCT and move toward an integrative, evolutionary-informed theory of family conflict. The present time may be especially favorable for such a paradigm shift, as signaled, for example, by the increasing success of life history theory and by the flourishing research on genomic imprinting and its psychological

implications. Our goal in this article was to make POCT more accessible to researchers with a psychological background, as well as to illustrate how the theory can inform (and potentially revolutionize) both theoretical and empirical research. We hope that we succeeded in our task, and that the reader will now share some of our excitement, both for the potential of POCT and for the future of our discipline.

References

- Abell, T. L., & Riely, C. A. (1992). Hyperemesis gravidarum. *Gastroenterology Clinics of North America*, *21*, 835–849.
- Ahluwalia, I. B., Morrow, B., & Hsia, J. (2005). Why do women stop breastfeeding? Findings from the pregnancy risk assessment and monitoring system. *Pediatrics*, *116*, 1408–1412. doi:10.1542/peds.2005-0013
- Ainsworth, M. D. S., Blehar, M. C., Waters, E., & Wall, S. (1978). *Patterns of attachment: A psychological study of the strange situation*. Hillsdale, NJ: Erlbaum.
- Allen, E. S., Horvath, S., Tong, F., Kraft, P., Spiteri, E., Riggs, A. D., & Marahrens, Y. (2003). High concentrations of long interspersed nuclear element sequence distinguish monoallelically expressed genes. *Proceedings of the National Academy of Sciences, USA*, *100*, 9940–9945. doi:10.1073/pnas.1737401100
- Altmann, J. (1980). *Baboon mothers and infants*. Cambridge, MA: Harvard University Press.
- American Diabetes Association. (2004). Gestational diabetes mellitus. *Diabetes Care*, *27*, s88–s90. doi:10.2337/diacare.27.2007.S88
- Andrews, P. W. (2006). Parent–offspring conflict and cost-benefit analysis in adolescent suicidal behavior: Effects of birth order and dissatisfaction with mother on attempt incident and severity. *Human Nature*, *17*, 190–211. doi:10.1007/s12110-006-1017-8
- Apicella, C. L., & Marlowe, F. W. (2004). Perceived mate fidelity and paternal resemblance predict men's investment in children. *Evolution and Human Behavior*, *25*, 371–378. doi:10.1016/j.evolhumbehav.2004.06.003
- Apicella, C. L., & Marlowe, F. W. (2007). Men's reproductive investment decisions. *Human Nature*, *18*, 22–34. doi:10.1007/BF02820844
- Apostolou, M. (2007a). Elements of parental choice: The evolution of parental preferences in relation to in-law selection. *Evolutionary Psychology*, *5*, 70–83.
- Apostolou, M. (2007b). Sexual selection under parental choice: The role of parents in the evolution of human mating. *Evolution and Human Behavior*, *28*, 403–409. doi:10.1016/j.evolhumbehav.2007.05.007
- Apostolou, M. (2008a). Parent–offspring conflict over mating: The case of beauty. *Evolutionary Psychology*, *6*, 303–315.
- Apostolou, M. (2008b). Parent–offspring conflict over mating: The case of family background. *Evolutionary Psychology*, *6*, 456–468.
- Apostolou, M. (2010). Sexual selection under parental choice in agropastoral societies. *Evolution and Human Behavior*, *31*, 39–47. doi:10.1016/j.evolhumbehav.2009.06.010
- Arck, P. C., Rose, M., Hertwig, K., Hagen, E., Hildebrandt, M., & Klapp, B. F. (2001). Stress and immune mediators in miscarriage. *Human Reproduction*, *16*, 1505–1511. doi:10.1093/humrep/16.7.1505
- Arnett, J. J. (1999). Adolescent storm and stress, reconsidered. *American Psychologist*, *54*, 317–326. doi:10.1037/0003-066X.54.5.317
- Arngrímsson, R. (2005). Epigenetics of hypertension in pregnancy. *Nature Genetics*, *37*, 460–461. doi:10.1038/ng0505-460
- Badcock, C. (2009). *Imprinted brain: How genes set the balance of the mind between autism and psychosis*. London, England: Jessica Kingsley.
- Barash, D. P., & Lipton, J. E. (2001). *The myth of monogamy: Fidelity and infidelity in animals and people*. New York, NY: Henry Holt and Company.
- Barratt, M., Roach, M. A., & Leavitt, L. A. (1996). The impact of low-risk

- prematurity on maternal behaviour and toddlers outcomes. *International Journal of Behavioral Development*, *19*, 581–602.
- Barrett, L., & Henzi, S. P. (2000). Are baboon infants Sir Phillip Sydney's offspring? *Ethology*, *106*, 645–658. doi:10.1046/j.1439-0310.2000.00577.x
- Bartolomei, M. S., & Tilghman, S. M. (1997). Genomic imprinting in mammals. *Annual Review of Genetics*, *31*, 493–525. doi:10.1146/annurev.genet.31.1.493
- Bateson, P. (1994). The dynamics of parent–offspring relationships in mammals. *Trends in Ecology and Evolution*, *9*, 399–403. doi:10.1016/0169-5347(94)90066-3
- Bateson, P., Barker, D., Clutton-Brock, T., Deb, D., D'Udine, B., Foley, R. A., . . . Sultan, S. E. (2004). Developmental plasticity and human health. *Nature*, *430*, 419–421. doi:10.1038/nature02725
- Beaudet, A. L., & Jiang, Y. (2002). A rheostat model for a rapid and reversible form of imprinting-dependent evolution. *American Journal of Human Genetics*, *70*, 1389–1397. doi:10.1086/340969
- Beaulieu, D. A., & Bugental, D. (2008). Contingent parental investment: An evolutionary framework for understanding early interaction between mothers and children. *Evolution and Human Behavior*, *29*, 249–255. doi:10.1016/j.evolhumbehav.2008.01.002
- Belsky, J. (1999). Modern evolutionary theory and patterns of attachment. In J. Cassidy & P. R. Shaver (Eds.), *Handbook of attachment: Theory, research, and clinical applications* (pp. 141–161). New York, NY: Guilford Press.
- Belsky, J., Steinberg, L., & Draper, P. (1991). Childhood experience, interpersonal development, and reproductive strategy: An evolutionary theory of socialization. *Child Development*, *62*, 647–670. doi:10.2307/1131166
- Berezkei, T., & Csanaky, A. (2001). Stressful family environment, mortality, and child socialization: Life-history strategies among adolescents and adults from unfavorable social circumstances. *International Journal of Behavioral Development*, *25*, 501–508. doi:10.1080/01650250042000573
- Berman, C. M., Rasmussen, K. L. R., & Suomi, S. J. (1993). Reproductive consequences of maternal care patterns during estrus among free-ranging rhesus monkeys. *Behavioral Ecology and Sociobiology*, *32*, 391–399. doi:10.1007/BF00168823
- Bogin, B. (1997). Evolutionary hypotheses for human childhood [Supplement: Yearbook of Physical Anthropology]. *American Journal of Physical Anthropology*, *104*, 63–89. doi:10.1002/(SICI)1096-8644(1997)25+<63::AID-AJPA3>3.0.CO;2-8
- Boney, C. M., Verma, A., Tucker, R., & Vohr, B. R. (2005). Metabolic syndrome in childhood: Association with birth weight, maternal obesity, and gestational diabetes mellitus. *Pediatrics*, *115*, e290–e296. doi:10.1542/peds.2004-1808
- Borgerhoff Mulder, M. (2000). Optimizing offspring: The quantity–quality trade-off in agropastoral Kipsigis. *Evolution & Human Behavior*, *21*, 391–410. doi:10.1016/S1090-5138(00)00054-4
- Bornstein, M. H., & Putnick, D. L. (2007). Chronological age, cognitions, and practices in European American mothers: A multivariate study of parenting. *Developmental Psychology*, *43*, 850–864. doi:10.1037/0012-1649.43.4.850
- Braza, F. (2004). Human parental investment affected by maternal age and parity. *Human Ecology*, *32*, 163–175. doi:10.1023/B:HUEC.0000019761.98723.af
- Briskie, J. V., Naugler, C. T., & Leech, S. M. (1994). Begging intensity of nestling birds varies with sibling relatedness. *Proceedings of the Royal Society B: Biological Sciences*, *258*, 73–78. doi:10.1098/rspb.1994.0144
- Brown, J., Cohen, P., Johnson, J. G., & Salzinger, S. (1998). A longitudinal analysis of risk factors for child maltreatment: Findings of a 17 year prospective study of officially recorded and self-reported child abuse and neglect. *Child Abuse & Neglect*, *22*, 1065–1078. doi:10.1016/S0145-2134(98)00087-8
- Brown, W. M., & Consedine, N. S. (2004). Just how happy is the happy puppet? An emotion signalling and kinship theory perspective on the behavioural phenotype of children with Angelman syndrome. *Medical Hypotheses*, *63*, 377–385. doi:10.1016/j.mehy.2004.05.010
- Bugental, D. B., Beaulieu, D. A., & Silbert-Geiger, A. (2010). Increases in parental investment and child health as a result of an early intervention. *Journal of Experimental Child Psychology*, *106*, 30–40. doi:10.1016/j.jecp.2009.10.004
- Bugental, D. B., & Happaney, K. (2004). Predicting infant maltreatment in low-income families: The interactive effects of maternal attribution of child status at birth. *Developmental Psychology*, *40*, 234–243. doi:10.1037/0012-1649.40.2.234
- Buhrmester, D. (1992). The developmental course of sibling peer relationships. In F. Boer & J. Dunn (Eds.), *Children's sibling relationships: Developmental and clinical issues* (pp. 19–40). Hillsdale, NJ: Erlbaum.
- Buhrmester, D., & Furman, W. (1990). Perceptions of sibling relationships during middle childhood and adolescence. *Child Development*, *61*, 1387–1398. doi:10.2307/1130750
- Buller, D. J. (2005). *Adapting minds*. Cambridge, MA: MIT Press.
- Burch, R. L., & Gallup, G. G., Jr. (2000). Perceptions of paternal resemblance predict family violence. *Evolution and Human Behavior*, *21*, 429–435. doi:10.1016/S1090-5138(00)00056-8
- Buunk, A. P., Park, J. H., & Dubbs, S. L. (2008). Parent–offspring conflict in mate preferences. *Review of General Psychology*, *12*, 47–62. doi:10.1037/1089-2680.12.1.47
- Buunk, A. P., & Solano, A. C. (2010). Conflicting preferences of parents and offspring over criteria for a mate: A study in Argentina. *Journal of Family Psychology*, *24*, 391–399. doi:10.1037/a0020252
- Cassidy, J., & Shaver, P. R. (Eds.). (2008). *Handbook of attachment* (2nd ed.). New York, NY: Guilford Press.
- Chisholm, J. S. (1999). *Death, hope, and sex: Steps to an evolutionary ecology of mind and morality*. Cambridge, England: Cambridge University Press.
- Ciricille, V. G. (1995). *Sibling relationships across the lifespan*. New York, NY: Plenum Press.
- Clutton-Brock, T. H. (1984). Reproductive effort and terminal investment in iteroparous animals. *The American Naturalist*, *123*, 212–229. doi:10.1086/284198
- Collins, W. A., & Laursen, B. (2006). Parent–adolescent relationships. In P. Noller (Ed.), *Close relationships: Functions, forms, and processes* (pp. 111–125). Hove, England: Psychology Press/Taylor & Francis.
- Crespi, B., & Badcock, C. (2008a). The evolutionary social brain: From genes to psychiatric conditions. *Behavioral and Brain Sciences*, *31*, 284–320. doi:10.1017/S0140525X08004457
- Crespi, B., & Badcock, C. (2008b). Psychosis and autism as diametrical disorders of the social brain. *Behavioral and Brain Sciences*, *31*, 241–261. doi:10.1017/S0140525X08004214
- Crespi, B., Stead, P., & Elliot, M. (2010). Comparative genomics of autism and schizophrenia. *Proceedings of the National Academy of Sciences, USA*, *107*(Suppl. 1), 1736–1741. doi:10.1073/pnas.0906080106
- Cunningham, A. S., Jelliffe, D. B., & Jelliffe, E. F. P. (1991). Breast-feeding and health in the 1980s: A global epidemiological review. *The Journal of Pediatrics*, *118*, 659–666. doi:10.1016/S0022-3476(05)80023-X
- Daly, M., & Wilson, M. (1980). Discriminative parental solicitude: A biological perspective. *Journal of Marriage and the Family*, *42*, 277–288. doi:10.2307/351225
- Daly, M., & Wilson, M. (1984). A sociobiological analysis of human infanticide. In G. Hausfater & S. B. Hrdy (Eds.), *Infanticide: Comparative and evolutionary perspectives* (pp. 487–502). Hawthorne, NY: Aldine.
- Daly, M., & Wilson, M. (1988). *Homicide*. Hawthorne, NY: Aldine.
- Daly, M., & Wilson, M. (2005). Reply to David Buller. Retrieved from

- <http://www.psych.ucsb.edu/research/cep/buller/reply%20to%20david%20buller.pdf>
- Daly, M., & Wilson, M. (2007). "Cinderella effect" controversial? A case study of evolution minded research and critiques thereof. In C. Crawford & D. Krebs (Eds.), *Foundations of evolutionary psychology* (pp. 383–400). Mahwah, NJ: Erlbaum.
- Davies, W., Isles, A. R., & Wilkinson, L. S. (2005). Imprinted gene expression in the brain. *Neuroscience and Biobehavioral Reviews*, *29*, 421–430. doi:10.1016/j.neubiorev.2004.11.007
- Davies, W., Lynn, P. M. Y., Relkovic, D., & Wilkinson, L. S. (2008). Imprinted genes and neuroendocrine function. *Frontiers in Neuroendocrinology*, *29*, 413–427. doi:10.1016/j.yfrne.2007.12.001
- De Goede, I. H. A., Branje, S. J. T., & Mees, W. H. J. (2009). Developmental changes in adolescents' perceptions of relationships with their parents. *Journal of Youth and Adolescence*, *38*, 75–88. doi:10.1007/s10964-008-9286-7
- Del Giudice, M. (2007). The evolutionary biology of cryptic pregnancy: A re-appraisal of the "denied pregnancy" phenomenon. *Medical Hypotheses*, *68*, 250–258. doi:10.1016/j.mehy.2006.05.066
- Del Giudice, M. (2009). Sex, attachment, and the development of reproductive strategies. *Behavioral and Brain Sciences*, *32*, 1–21. doi:10.1017/S0140525X09000016
- Del Giudice, M., Angeleri, R., Brizio, A., & Elena, M. R. (2010). The evolution of autistic-like and schizotypal traits: A sexual selection hypothesis. *Frontiers in Psychology*, *1*, Article 41. doi:10.3389/fpsyg.2010.00041
- Del Giudice, M., Angeleri, R., & Manera, V. (2009). The juvenile transition: A developmental switch point in human life history. *Developmental Review*, *29*, 1–31. doi:10.1016/j.dr.2008.09.001
- Del Giudice, M., & Belsky, J. (2010). Sex differences in attachment emerge in middle childhood: An evolutionary hypothesis. *Child Development Perspectives*, *4*, 97–105. doi:10.1111/j.1750-8606.2010.00125.x
- Del Giudice, M., & Belsky, J. (2011a). The development of life history strategies: Toward a multi-stage theory. In D. M. Buss & P. H. Hawley (Eds.), *The evolution of personality and individual differences* (pp. 154–176). New York, NY: Oxford University Press.
- Del Giudice, M., & Belsky, J. (2011b). Parent-child relationships. In C. Salmon & T. Shackelford (Eds.), *The Oxford handbook of evolutionary family psychology* (pp. 65–82). New York, NY: Oxford University Press.
- Dickins, B. J. A., Dickins, D. W., & Dickins, T. E. (2008). Is this conjectural phenotypic dichotomy a plausible outcome of genomic imprinting? *Behavioral and Brain Sciences*, *31*, 267–268. doi:10.1017/S0140525X08004287
- Draper, P., & Harpending, H. (1988). A sociobiological perspective on the development of human reproductive strategies. In K. MacDonald (Ed.), *Sociobiological perspectives on human development* (pp. 340–372). Lincoln, NE: Springer-Verlag.
- Drummond, H. (2001). A reevaluation of the role of food in broodmate aggression. *Animal Behaviour*, *61*, 517–526. doi:10.1006/anbe.2000.1641
- Dunn, J., Slomkowski, C., & Beardsall, L. (1994). Sibling relationship from preschool period through middle childhood and early adolescence. *Developmental Psychology*, *30*, 315–324. doi:10.1037/0012-1649.30.3.315
- Easterling, T. R., Benedetti, T. J., Schmucker, B. C., & Millard, S. P. (1990). Maternal hemodynamics in normal and preeclamptic pregnancies: A longitudinal study. *Obstetrics and Gynecology*, *76*, 1061–1069.
- Ellis, B. J., Dahl, R. E., Del Giudice, M., Figueredo, A. J., Gray, P., Griskevicius, V., . . . Wilson, D. S. (2011). *The evolutionary basis of risky adolescent behavior: Implications for science, policy, and practice*. Manuscript submitted for publication.
- Ellis, B. J., Figueredo, A. J., Brumbach, B. H., & Schlomer, G. L. (2009). Fundamental dimensions of environmental risk: The impact of harsh versus unpredictable environments on the evolution and development of life history strategies. *Human Nature*, *20*, 204–268. doi:10.1007/s12110-009-9063-7
- Ellison, P. T. (2001). *On fertile ground: A natural history of human reproduction*. Cambridge, MA: Harvard University Press.
- Ellis-Schwabe, M., & Thornburg, H. D. (1986). Conflict areas between parents and their adolescents. *The Journal of Psychology: Interdisciplinary and Applied*, *120*, 59–68. doi:10.1080/00223980.1986.9712616
- El-Sheikh, M., & Elmore-Staton, L. (2004). The link between marital conflict and child adjustment: Parent-child conflict and perceived attachments as mediators, potentiators, and mitigators of risk. *Development and Psychopathology*, *16*, 631–648. doi:10.1017/S0954579404004705
- El-Sheikh, M., & Flanagan, E. (2001). Parental problem drinking and children's adjustment: Family conflict and parental depression as mediators and moderators of risk. *Journal of Abnormal Child Psychology*, *29*, 417–432. doi:10.1023/A:1010447503252
- Feig, D. S., Zinman, B., Wang, X., & Hux, J. E. (2008). Risk of development of diabetes mellitus after diagnosis of gestational diabetes. *Canadian Medical Association Journal*, *179*, 229–234. doi:10.1503/cmaj.080012
- Fessler, D. M. T., Navarrete, C. D., Hopkins, W., & Izard, M. K. (2005). Examining the terminal investment hypothesis in humans and chimpanzees: Associations among maternal age, parity, and birth weight. *American Journal of Physical Anthropology*, *127*, 95–104. doi:10.1002/ajpa.20039
- Fisher, R. A. (1930). *The genetical theory of natural selection*. Oxford, England: Clarendon Press.
- Flaxman, S. M., & Sherman, P. W. (2000). Morning sickness: A mechanism for protecting mother and embryo. *Quarterly Review of Biology*, *75*, 113–148. doi:10.1086/393377
- Flaxman, S. M., & Sherman, P. W. (2008). Morning sickness: Adaptive cause or nonadaptive consequence of embryo viability? *The American Naturalist*, *172*, 54–62. doi:10.1086/588081
- Forbes, L. S. (1997). The evolutionary biology of spontaneous abortion in humans. *Trends in Ecology and Evolution*, *12*, 446–450. doi:10.1016/S0169-5347(97)01179-8
- Forbes, S. (2002). Pregnancy sickness and embryo quality. *Trends in Ecology and Evolution*, *17*, 115–120. doi:10.1016/S0169-5347(01)02428-4
- Fouts, H. N. (2004). Social and emotional contexts of weaning among Bofi farmers and foragers. *Ethnology*, *43*, 65–81. doi:10.2307/3773856
- Fouts, H. N., Hewlett, B. S., & Lamb, M. E. (2005). Parent-offspring weaning conflicts among the Bofi farmers and foragers in central Africa. *Current Anthropology*, *46*, 29–50. doi:10.1086/425659
- Geary, D. C. (2000). Evolution and proximate expression of human paternal investment. *Psychological Bulletin*, *126*, 55–77. doi:10.1037/0033-2909.126.1.55
- Gluckman, P. D., Hanson, M. A., & Beedle, A. S. (2007). Early life events and their consequences for later disease: A life history and evolutionary perspective. *American Journal of Human Biology*, *19*, 1–19. doi:10.1002/ajhb.20590
- Godfray, H. C. J. (1991, July 25). The signaling of need by offspring to their parents. *Nature*, *352*, 328–330. doi:10.1038/352328a0
- Godfray, H. C. J. (2002, July 13). Evolutionary theory of parent-offspring conflict. *Nature*, *376*, 133–138. doi:10.1038/376133a0
- Goldberg, S., Perrotta, M., Minde, K., & Corter, V. (1986). Maternal behavior and attachment in low-birth-weight twins and singletons. *Child Development*, *57*, 34–46. doi:10.2307/1130635
- Gomendio, M. (1991). Parent/offspring conflict and maternal investment in rhesus macaques. *Animal Behaviour*, *42*, 993–1005. doi:10.1016/S0003-3472(05)80152-6
- Goshen, R., Gonik, B., de Groot, N., & Hochberg, A. A. (1994). The genomic basis of the beta-subunit of human chorionic gonadotropin

- diversity in triploidy. *American Journal of Obstetrics and Gynecology*, 170, 700–701.
- Gottlander, K. (1987). Parental feeding-behavior and sibling competition in the pied fly catcher *ficedula-hypoleuca*. *Ornis Scandinavica*, 18, 269–276. doi:10.2307/3676895
- Grafen, A. (1985). A geometric view of relatedness. *Oxford Surveys in Evolutionary Biology*, 2, 28–90.
- Gray, S. J. (1996). Ecology of weaning among nomadic Turkana pastoralists of Kenya: Maternal thinking, maternal behavior, and human adaptive strategies. *Human Biology*, 68, 437–465.
- Gregg, C., Zhang, J., Weissbourd, B., Luo, S., Schroth, G. P., Haig, D., & Dulac, C. (2010, August 6). High-resolution analysis of parent-of-origin allelic expression in the mouse brain. *Science*, 329, 643–648. doi:10.1126/science.1190830
- Guttman, N., & Zimmerman, D. R. (2000). Low-income mothers' views on breastfeeding. *Social Science & Medicine*, 50, 1457–1473. doi:10.1016/S0277-9536(99)00387-1
- Hagen, E. H., Barrett, H. C., & Price, M. E. (2006). Do human parents face a quantity–quality tradeoff? Evidence from the Shuar community. *American Journal of Physical Anthropology*, 130, 405–418. doi:10.1002/ajpa.20272
- Haig, D. (1993). Genetic conflicts in human pregnancy. *Quarterly Review of Biology*, 68, 495–532. doi:10.1086/418300
- Haig, D. (1996). Placental hormones, genomic imprinting, and maternal–fetal communication. *Journal of Evolutionary Biology*, 9, 357–380. doi:10.1046/j.1420-9101.1996.9030357.x
- Haig, D. (1997). Parental antagonism, relatedness asymmetries, and genomic imprinting. *Proceedings of the Royal Society B: Biological Sciences*, 264, 1657–1662. doi:10.1098/rspb.1997.0230
- Haig, D. (2004). Genomic imprinting and kinship: How good is the evidence? *Annual Review of Genetics*, 38, 553–585. doi:10.1146/annurev.genet.37.110801.142741
- Haig, D. (2010). Transfers and transitions: Parent–offspring conflict, genomic imprinting, and the evolution of human life history. *Proceedings of the National Academy of Sciences, USA*, 107, 1731–1735. doi:10.1073/pnas.0904111106
- Haig, D., & Wharton, R. (2003). Prader-Willi syndrome and the evolution of human childhood. *American Journal of Human Biology*, 15, 320–329. doi:10.1002/ajhb.10150
- Haig, D., & Wilkins, J. F. (2000). Genomic imprinting, sibling solidarity, and the logic of collective action. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 355, 1593–1597. doi:10.1098/rstb.2000.0720
- Hamilton, W. D. (1964). The genetical evolution of social behaviour. *Journal of Theoretical Biology*, 7, 1–16. doi:10.1016/0022-5193(64)90038-4
- Hetherington, M. E., & Clingempeel, W. G. (1992). Coping with marital transitions: A family systems perspective. *Monographs of the Society for Research on Child Development*, 57(2–3, Serial No. 227).
- Hetherington, M. E., Henderson, S. H., & Reiss, D. (1999). Adolescent siblings in stepfamilies: Family functioning and adolescent adjustment. *Monographs of the Society for Research on Child Development*, 64(4, Serial No. 259).
- Hofer, H., & East, M. L. (1995). Virilized sexual genitalia as adaptations of female spotted hyenas. *Revue Suisse De Zoologie*, 102, 895–906.
- Hofer, H., & East, M. L. (2008). Siblicide in Serengeti spotted hyenas: A long-term study of maternal input and cub survival. *Behavioral Ecology and Sociobiology*, 62, 341–351. doi:10.1007/s00265-007-0421-3
- Hoffman, C. L., Higham, J. P., Mas-Rivera, A., Ayala, J. E., & Maestripieri, D. (2010). Terminal investment and senescence in rhesus macaques (*Macaca mulatta*) on Cayo Santiago. *Behavioral Ecology*, 21, 972–978. doi:10.1093/beheco/arq098
- Hrdy, S. B. (1999). *Mother nature: Maternal instincts and how they shape the human species*. New York, NY: Ballantine.
- Huizink, A. C., de Medina, P. G., Mulder, E. J., Visser, G. H., & Buitelaar, J. K. (2002). Psychological measures of prenatal stress as predictors of infant temperament. *Journal of the American Academy of Child & Adolescent Psychiatry*, 41, 1078–1085. doi:10.1097/00004583-200209000-00008
- Isles, A. R., Davies, W., & Wilkinson, L. S. (2006). Genomic imprinting and the social brain. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 361, 2229–2237. doi:10.1098/rstb.2006.1942
- Jankowiak, W., & Diderich, M. (2000). Sibling solidarity in a polygamous community in the USA: Unpacking inclusive fitness. *Evolution and Human Behavior*, 21, 125–139. doi:10.1016/S1090-5138(00)00027-1
- Johnstone, R. A. (1996). Begging signals and parent–offspring conflict: do parents always win? *Proceedings of the Royal Society B: Biological Sciences*, 263, 1677–1681. doi:10.1098/rspb.1996.0245
- Kaplan, H. S., & Lancaster, J. B. (2003). An evolutionary and ecological analysis of human fertility, mating patterns, and parental investment. In K. W. Wachter & R. A. Bulatao (Eds.), *Offspring: Human fertility behavior in biodemographic perspective* (pp. 170–223). Washington, DC: The National Academies Press.
- Keller, M. C. (2008). Problems with the imprinting hypothesis of schizophrenia and autism. *Behavioral and Brain Sciences*, 31, 273–274. doi:10.1017/S0140525X08004342
- Kelsey, G. (2011). Epigenetics and the brain: Transcriptome sequencing reveals new depths to genomic imprinting. *BioEssays*, 33, 362–367.
- Khashan, A. S., Abel, K. M., McNamee, R., Pedersen, M. G., Webb, R. T., Baker, P. N., . . . Mortensen, P. B. (2008). Higher risk of offspring schizophrenia following antenatal maternal exposure to severe adverse life events. *Archives of General Psychiatry*, 65, 146–152. doi:10.1001/archgenpsychiatry.2007.20
- Kilner, R. (1995). When do canary parents respond to nestling signals of need? *Proceedings of the Royal Society B: Biological Sciences*, 260, 343–348. doi:10.1098/rspb.1995.0102
- Kim, K. J., Conger, R. D., Lorenz, F. O., & Elder, G. H., Jr. (2001). Parent–adolescent reciprocity in negative affect and its relation to early adult social development. *Developmental Psychology*, 37, 775–790. doi:10.1037/0012-1649.37.6.775
- Klomp, H. (1970). Determination of clutch size in birds: A review. *Ardea*, 58, 1–124.
- Kölliker, M. (2003). Estimating mechanisms and equilibria for offspring begging and parental provisioning. *Proceedings of the Royal Society B: Biological Sciences*, 270, S110–S113. doi:10.1098/rsbl.2003.0032
- Kölliker, M., Brodie, E. D., III, & Moore, A. (2005). The coadaptation of parental supply and offspring demand. *The American Naturalist*, 166, 506–516. doi:10.1086/491687
- Kölliker, M., & Richner, H. (2001). Parent–offspring conflict and the genetics of offspring solicitation and parental response. *Animal Behaviour*, 62, 395–407. doi:10.1006/anbe.2001.1792
- Konner, M. (2005). Hunter-gatherer infancy and childhood: The !Kung and others. In B. S. Hewlett & M. E. Lamb (Eds.), *Hunter-gatherer childhoods* (pp. 19–64). New Brunswick, NJ: Transaction.
- Kushnick, G. (2009). Parental supply and offspring demand amongst Karo Batak mothers and children. *Journal of Biosocial Science*, 41, 183–193.
- Kuzawa, C. W. (2005). Fetal origins of developmental plasticity: Are fetal cues reliable predictors of future nutritional environments? *American Journal of Human Biology*, 17, 5–21. doi:10.1002/ajhb.20091
- Kuzawa, C. W. (2007). Developmental origins of life history: Growth, productivity, and reproduction. *American Journal of Human Biology*, 19, 654–661. doi:10.1002/ajhb.20659
- Langer, O., Yogeve, Y., Most, O., & Xenakis, E. M. J. (2005). Gestational diabetes: The consequences of not treating. *American Journal of Obstetrics and Gynecology*, 192, 989–997. doi:10.1016/j.ajog.2004.11.039
- Laursen, B., & Collins, A. (1994). Interpersonal conflict during adolescence. *Psychological Bulletin*, 115, 197–209. doi:10.1037/0033-2909.115.2.197

- Laursen, B., Coy, K. C., & Collins, W. A. (1998). Reconsidering changes in parent-child conflict across adolescence: A meta-analysis. *Child Development, 69*, 817-832.
- Lawson, D. W., & Mace, R. (2009). Trade-offs in modern parenting: A longitudinal study of sibling competition for parental care. *Evolution and Human Behavior, 30*, 170-183. doi:10.1016/j.evolhumbehav.2008.12.001
- Leonard, M., & Horn, A. (1996). Provisioning rules in tree swallows. *Behavioral Ecology and Sociobiology, 38*, 341-347. doi:10.1007/s002650050250
- Lessells, C. M., & Parker, G. A. (1999). Parent-offspring conflict: The full-sib-half-sib fallacy. *Proceedings of the Royal Society B: Biological Sciences, 266*, 1637-1643. doi:10.1098/rspb.1999.0826
- Lind, T., & Aspillaga, M. (1988). Metabolic changes during normal and diabetic pregnancy. In E. A. Reece & D. R. Coustan (Eds.), *Diabetes mellitus in pregnancy: Principles and practice* (pp. 75-102). New York, NY: Churchill Livingstone.
- Lindheimer, M. D., Taler, S. J., & Cunningham, F. G. (2008). Hypertension in pregnancy. *Journal of the American Society of Hypertension, 2*, 484-494. doi:10.1016/j.jash.2008.10.001
- Long, T. A. F. (2005). The influence of mating system on the intensity of parent-offspring conflict in primates. *Journal of Evolutionary Biology, 18*, 509-515. doi:10.1111/j.1420-9101.2005.00888.x
- Luke, B., & Brown, M. B. (2007). Maternal risk factors for potential maltreatment deaths among healthy singleton and twin infants. *Twin Research and Human Genetics, 10*, 778-785. doi:10.1375/twin.10.5.778
- Maestripieri, D. (2002). Parent-offspring conflict in primates. *International Journal of Primatology, 23*, 923-951. doi:10.1023/A:1015537201184
- Malkin, C. M., & Lamb, M. E. (1994). Child maltreatment: A test of sociobiological theory. *Journal of Comparative Family Studies, 25*, 121-133.
- Mann, J. (1992). Nurture or neglect: Maternal psychology and behavioural preference among preterm twins. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 367-390). New York, NY: Oxford University Press.
- Marlowe, F. W. (2003). The mating system of foragers in the Standard Cross-Cultural Sample. *Cross-Cultural Research, 37*, 282-306. doi:10.1177/1069397103254008
- McCarton, C. M., Wallace, I. F., Divon, M., & Vaughan, H. G., Jr. (1996). Cognitive and neurologic development of the premature, small for gestational age infant through age 6: Comparison by birth weight and gestational age. *Pediatrics, 98*, 1167-1178.
- McDade, T. W., & Worthman, C. M. (1998). The weanling's dilemma reconsidered: A biocultural analysis of breastfeeding ecology. *Journal of Developmental and Behavioral Pediatrics, 19*, 286-299. doi:10.1097/00004703-199808000-00008
- McGue, M., Elkins, I., Walden, B., & Iacono, W. G. (2005). Perceptions of the parent-adolescent relationship: A longitudinal investigation. *Developmental Psychology, 41*, 971-984. doi:10.1037/0012-1649.41.6.971
- Meaney, M. J. (2010). Epigenetics and the biological definition of gene \times environment interactions. *Child Development, 81*, 41-79. doi:10.1111/j.1467-8624.2009.01381.x
- Mendl, M. (1988). The effects of litter size variation on mother-offspring relationships and behavioral and physical development in several mammalian species (principally rodents). *Journal of Zoology, 215*, 15-34. doi:10.1111/j.1469-7998.1988.tb04882.x
- Mendl, M. (1994). How should parents respond to a reduction in litter size: Abandonment or extra care? *Behavioural Processes, 31*, 285-291. doi:10.1016/0376-6357(94)90013-2
- Mersky, J. P., Berger, L. M., Reynolds, A. J., & Gromoske, A. N. (2009). Risk factors for child and adolescent maltreatment: A longitudinal investigation of a cohort of inner-city youth. *Child Maltreatment, 14*, 73-88. doi:10.1177/1077559508318399
- Miller, G. F. (2000). *The mating mind. How sexual choice shaped the evolution of human nature*. London, England: Heinemann.
- Möhler, E., Parzer, P., Brunner, R., Wiebel, A., & Resch, F. (2006). Emotional stress in pregnancy predicts human infant reactivity. *Early Human Development, 82*, 731-737. doi:10.1016/j.earlhumdev.2006.02.010
- Montemayor, R. (1986). Family variation in parent-adolescent storm and stress. *Journal of Adolescent Research, 1*, 15-31. doi:10.1177/074355488611003
- Moore, M. P., & Redman, C. W. G. (1983). Case-control study of severe pre-eclampsia of early onset. *British Medical Journal, 287*, 580-583. doi:10.1136/bmj.287.6392.580
- Moreno-Rueda, G., Soler, M., Soler, J. J., Martínez, J. G., & Pérez-Contreras, T. (2007). Rules of food allocation between nestlings of the black billed magpie *pica pica*, a species showing brood reduction. *Ardeola, 54*, 15-25.
- Nepomnaschy, P. A., Welch, K. B., McConnell, D. S., Low, B. S., Strassmann, B. I., & England, B. G. (2006). Cortisol levels and very early pregnancy loss in humans. *Proceedings of the National Academy of Sciences, USA, 103*, 3938-3942. doi:10.1073/pnas.0511183103
- Nettle, D. (2010). Dying young and living fast: Variation in life history across English neighborhoods. *Behavioral Ecology, 21*, 387-395. doi:10.1093/beheco/arp202
- O'Connor, T. G., Dunn, J., Jenkins, J. M., & Rashash, J. (2006). Predictors of between-family and within-family variation in parent-child relationships. *Journal of Child Psychology and Psychiatry, 47*, 498-510. doi:10.1111/j.1469-7610.2005.01527.x
- Ogbuanu, C. A., Probst, J., Laditka, S. B., Liu, J., Baek, J., & Glover, S. (2009). Reasons why women do not initiate breastfeeding: A southeastern study. *Women's Health Issues, 19*, 268-278. doi:10.1016/j.whi.2009.03.005
- Oudejans, C. M. B., & van Dijk, M. (2008). Placental gene expression and pre-eclampsia. *Placenta, 29*, 78-82. doi:10.1016/j.placenta.2007.09.005
- Overpeck, M. D., Brenner, R. A., Trumble, A. C., Trifiletti, L. B., & Berendes, H. W. (1998). Risk factors for infant homicide in the United States. *The New England Journal of Medicine, 339*, 1211-1216. doi:10.1056/NEJM199810223391706
- Paikoff, R. L., & Brooks-Gunn, J. (1991). Do parent-child relationships change during puberty? *Psychological Bulletin, 110*, 47-66. doi:10.1037/0033-2909.110.1.47
- Parker, G. A. (1985). Models of parent-offspring conflict: V. Effects of the behaviour of the two parents. *Animal Behaviour, 33*, 519-533. doi:10.1016/S0003-3472(85)80075-0
- Parker, G. A., & Macnair, M. R. (1979). Models of parent-offspring conflict: IV. Suppression: Evolutionary retaliation by the parents. *Animal Behaviour, 27*, 1210-1235. doi:10.1016/0003-3472(79)90068-X
- Parker, G. A., Mock, D. W., & Lamey, T. C. (1989). How selfish should stronger sibs be? *The American Naturalist, 133*, 846-868. doi:10.1086/284956
- Parker, G. A., Royle, N. J., & Hartley, I. R. (2002). Intrafamilial conflict and parental investment: A synthesis. *Philosophical Transactions of the Royal Society B: Biological Sciences, 357*, 295-307. doi:10.1098/rstb.2001.0950
- Pavé, R., Kowalewski, M. M., Paker, S. M., & Zunino, G. E. (2010). Preliminary study of mother-offspring conflict in black and gold howler monkeys (*Alouatta caraya*). *Primates, 51*, 221-226. doi:10.1007/s10329-010-0189-3
- Pepper, G. V., & Roberts, S. C. (2006). Rates of nausea and vomiting in pregnancy and dietary characteristics across populations. *Proceedings of the Royal Society B: Biological Sciences, 273*, 2675-2679. doi:10.1098/rspb.2006.3633
- Pickler, R. H. (2009). Understanding, promoting, and measuring effects of

- mother–infant attachment during infant feeding. *Journal of Obstetric, Gynecologic, & Neonatal Nursing*, 38, 468–469. doi:10.1111/j.1552-6909.2009.01043.x
- Pollet, T. V. (2007). Genetic relatedness and sibling relationship characteristics in a modern society. *Evolution and Human Behavior*, 28, 176–185. doi:10.1016/j.evolhumbehav.2006.10.001
- Profet, M. (1992). Pregnancy sickness as adaptation: A deterrent to maternal ingestion of teratogens. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind* (pp. 327–365). Oxford, England: Oxford University Press.
- Pruett, C. L., Calsyn, R. J., & Jensen, F. M. (1993). Social support received by children in stepmother, stepfather, and intact families. *Journal of Divorce & Remarriage*, 19, 165–180. doi:10.1300/J087v19n03_11
- Pryce, C. R. (1995). Determinants of motherhood in human and nonhuman primates: A biosocial model. In C. R. Pryce, R. D. Martin, & D. Skuse (Eds.), *Motherhood in human and nonhuman primates: Symposium conducted at the 3rd Schultz-Biegert Symposium* (pp. 1–15). Kartaue, Ittigen, Switzerland: Basel/Karger.
- Pugesek, B. H. (1990). Parental effort in the California gull: Tests of parent–offspring conflict theory. *Behavioral Ecology and Sociobiology*, 27, 211–215. doi:10.1007/BF00180305
- Pugesek, B. H. (1995). Offspring growth in the California gull: Reproductive effort and parental experience hypothesis. *Animal Behaviour*, 49, 641–647.
- Pugesek, B. H., & Deim, K. L. (1990). The relationship between reproduction and survival in known-aged California gulls. *Ecology*, 71, 811–817. doi:10.2307/1940332
- Quinlan, R. J. (2007). Human parental effort and environmental risk. *Proceedings of the Royal Society B: Biological Sciences*, 274, 121–125. doi:10.1098/rspb.2006.3690
- Quinlan, R. J., Quinlan, M. B., & Flinn, M. V. (2003). Parental investment and age at weaning in a Caribbean village. *Evolution and Human Behavior*, 24, 1–16. doi:10.1016/S1090-5138(02)00104-6
- Ragozin, A. S., Basham, R. B., Crnic, K. A., Greenberg, M. T., & Robinson, N. M. (1982). Effects of maternal age on parenting role. *Developmental Psychology*, 18, 627–634. doi:10.1037/0012-1649.18.4.627
- Renk, K., Liljequist, L., Simpson, J. E., & Phares, V. (2005). Gender and age differences in the topics of parent–adolescent conflict. *The Family Journal*, 13, 139–149. doi:10.1177/1066480704271190
- Robson, A., & Cline, B. (1998). Developmental consequences of intrauterine growth retardation. *Infant Behavior and Development*, 21, 331–344. doi:10.1016/S0163-6383(98)90010-8
- Roff, D. A. (1992). *The evolution of life histories: Theory and analysis*. New York, NY: Chapman and Hall.
- Ros, H. S., Cnattingius, S., & Lipworth, L. (1998). Comparison of risk factors for preeclampsia and gestational hypertension in a population-based cohort study. *American Journal of Epidemiology*, 147, 1062–1070.
- Ross, G. (2006). Diabetes mellitus. *Australian Family Physician*, 35, 392–396.
- Royce, N. J., Hartley, I. R., & Parker, G. A. (2002, April 18). Sexual conflict reduces offspring fitness in zebra finches. *Nature*, 416, 733–736. doi:10.1038/416733a
- Royce, N. J., Hartley, I. R., & Parker, G. A. (2004). Parental investment and family dynamics: Interactions between theory and empirical tests. *Population Ecology*, 46, 231–241. doi:10.1007/s10144-004-0196-6
- Schalkwyk, L. C., Meaburn, E. L., Smith, R., Dempster, E. L., Jeffries, A. R., Davies, M. N., . . . Mill, J. (2010). Allelic skewing of DNA methylation is widespread across the genome. *American Journal of Human Genetics*, 86, 196–212. doi:10.1016/j.ajhg.2010.01.014
- Scheper-Hughes, N. (1992). *Death without weeping: The violence of everyday life in Brazil*. Berkeley, CA: University of California Press.
- Schlomer, G. L., Ellis, B. J., & Garber, J. (2010). Mother–child conflict and sibling relatedness: A test of hypotheses from parent–offspring conflict theory. *Journal of Research on Adolescence*, 20, 287–306. doi:10.1111/j.1532-7795.2010.00641.x
- Schnitzer, P. G., & Ewigman, B. G. (2005). Child deaths resulting from inflicted injuries: Household risk factors and perpetrator characteristics. *Pediatrics*, 116, e687–e693. doi:10.1542/peds.2005-0296
- Scott-Phillips, T. C., Dickins, T. E., & West, S. A. (2011). Evolutionary theory and the ultimate–proximate distinction in the human behavioral sciences. *Perspectives on Psychological Science*, 6, 38–47. doi:10.1177/1745691610393528
- Sear, R. (2011). Parenting and families. In V. Swami (Ed.), *Evolutionary psychology: A critical introduction* (pp. 216–250). Oxford, England: Wiley-Blackwell.
- Smetana, J. G. (1989). Adolescents’ and parents’ reasoning about actual family conflict. *Child Development*, 60, 1052–1067.
- Smetana, J. G. (2005). Adolescent–parent conflict: Resistance and subversion as developmental process. In L. Nucci (Ed.), *Conflict, contradiction, and contrarian elements in moral development and education* (pp. 69–91). Mahwah, NJ: Erlbaum.
- Smetana, J., & Gains, C. (1999). Adolescent–parent conflict in middle-class African American families. *Child Development*, 70, 1447–1463. doi:10.1111/1467-8624.00105
- Smetana, J. G., Yau, J., Restrepo, A., & Braeges, J. L. (1991). Adolescent–parent conflict in married and divorced families. *Developmental Psychology*, 27, 1000–1010. doi:10.1037/0012-1649.27.6.1000
- Smiseth, P. T., Wright, J., & Kölliker, M. (2008). Parent–offspring conflict and coadaptation: Behavioural ecology meets quantitative genetics. *Proceedings of the Royal Society B: Biological Sciences*, 275, 1823–1830. doi:10.1098/rspb.2008.0199
- Smith, M. A. M. (2007). *Similarities and differences between adolescent monozygotic and dizygotic twins’ quality of the sibling relationship* (Doctoral dissertation). Available from ProQuest Dissertations and Theses database. (UMI No. 3284734)
- Soltis, J. (2004). The signal functions of early infant crying. *Behavioral and Brain Sciences*, 27, 443–458.
- Stamps, J., Clark, A., Arrowood, P., & Kus, B. (1985). Parent–offspring conflict in budgerigars. *Behaviour*, 94, 1–39. doi:10.1163/156853985X00253
- Steinberg, L. (1989). Pubertal maturation and parent–adolescent distance: An evolutionary perspective. In G. R. Adams, R. Moneta, & T. P. Gullotta (Eds.), *Biology of adolescent behavior and development* (pp. 71–97). Newbury Park, CA: Sage.
- Steinberg, L. (2001). We know some things: Parent–adolescent relationships in retrospect and prospect. *Journal of Research on Adolescence*, 11, 1–19. doi:10.1111/1532-7795.00001
- Sterns, S. C. (1992). *The evolution of life histories*. New York, NY: Oxford University Press.
- Strassmann, B. I., & Gillespie, B. (2002). Life-history theory, fertility and reproductive success in humans. *Proceedings of the Royal Society B: Biological Sciences*, 269, 553–562. doi:10.1098/rspb.2001.1912
- Sulloway, F. J. (1996). *Born to rebel: Birth order, family dynamics, and revolutionary genius*. New York, NY: Pantheon.
- Symonds, E. M. (1980). Aetiology of pre-eclampsia: A review. *Journal of the Royal Society of Medicine*, 73, 871–875.
- Temrin, H., Buchmayer, S., & Enquist, M. (2000). Step-parents and infanticide: New data contradict evolutionary predictions. *Proceedings of the Royal Society B: Biological Sciences*, 267, 943–945. doi:10.1098/rspb.2000.1094
- Temrin, H., Nordlund, J., Rying, M., & Tullberg, B. S. (2011). Is the higher rate of parental child homicide in stepfamilies an effect of non-genetic relatedness? *Current Zoology*, 57, 253–259.
- Thakkar, K. N., Matthews, N., & Park, S. (2008). A complete theory of psychosis and autism as diametric disorders of social brain must con-

- sider full range of clinical syndromes. *Behavioral and Brain Sciences*, 31, 277–278. doi:10.1017/S0140525X0800438X
- Thornhill, R., & Gangestad, S. W. (1993). Human facial beauty: Average-ness, symmetry, and parasite resistance. *Human Nature*, 4, 237–269. doi:10.1007/BF02692201
- Thornhill, R., & Møller, A. P. (1997). Developmental stability, disease, and medicine. *Biological Reviews*, 72, 497–548. doi:10.1017/S0006323197005082
- Tooley, G. A., Karakis, M., Stokes, M., & Ozanne-Smith, J. (2006). Generalising the Cinderella effect to unintentional childhood fatalities. *Evolution and Human Behavior*, 27, 224–230. doi:10.1016/j.evolhumbehav.2005.10.001
- Trillmich, F., & Wolf, J. B. W. (2008). Parent–offspring and sibling conflict in Galápagos fur seals and sea lions. *Behavioral Ecology and Sociobiology*, 62, 363–375. doi:10.1007/s00265-007-0423-1
- Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man: 1871–1971* (pp. 136–179). Chicago, IL: Aldine Atherton.
- Trivers, R. L. (1974). Parent–offspring conflict. *American Zoologist*, 14, 249–264.
- Trumbo, S. T. (1996). Parental care in invertebrates. *Advances in the Study of Behavior*, 25, 3–51. doi:10.1016/S0065-3454(08)60329-0
- Úbeda, F. (2008). Evolution of genomic imprinting with biparental care: Implications for Prader-Willi and Angelman syndromes. *PLoS Biology*, 6, e208. doi:10.1371/journal.pbio.0060208
- Úbeda, F., & Gardner, A. (2010). A model for genomic imprinting in the social brain: Juveniles. *Evolution*, 64, 2587–2600. doi:10.1111/j.1558-5646.2010.01015.x
- Úbeda, F., & Wilkins, J. F. (2008). Imprinted genes and human disease: An evolutionary perspective. *Advances in Experimental Medicine and Biology*, 626, 101–115. doi:10.1007/978-0-387-77576-0_8
- Van den Bergh, B. R. H., & Marcoen, A. (2004). High antenatal maternal anxiety is related to ADHD symptoms, externalizing problems, and anxiety in 8- and 9-year-olds. *Child Development*, 75, 1085–1097. doi:10.1111/j.1467-8624.2004.00727.x
- Van den Bergh, B. R. H., Mulder, E. J. H., Mennes, M., & Glover, V. (2005). Antenatal maternal anxiety and stress and the neurobehavioural development of the fetus and child: Links and possible mechanisms. A review. *Neuroscience and Biobehavioral Reviews*, 29, 237–258. doi:10.1016/j.neubiorev.2004.10.007
- Volk, A. A., & Quinsey, V. L. (2007). Parental investment resemblance: Replications, refinements, and revisions. *Evolutionary Psychology*, 5, 1–14.
- Weladji, R. B., Holand, Ø., Gaillard, J., Yoccoz, N. G., Mysterud, A., Nieminen, M., & Stenseth, N. C. (2010). Age-specific changes in different components of reproductive output in female reindeer: Terminal allocation or senescence? *Oecologia*, 162, 261–271. doi:10.1007/s00442-009-1443-5
- Wessel, J., Endrikat, J., & Büscher, U. (2002). Frequency of denial of pregnancy: Results and epidemiological significance of a 1-year prospective study in Berlin. *Acta Obstetrica et Gynaecologica Scandinavica*, 81, 1021–1027. doi:10.1034/j.1600-0412.2002.811105.x
- White, P. A. (2008). Maternal response to neonatal sibling conflict in the spotted hyena, *Crocuta crocuta*. *Behavioral Ecology and Sociobiology*, 62, 353–361. doi:10.1007/s00265-007-0422-2
- Whittingham, L. A., Dunn, P. O., & Clotfelter, E. D. (2003). Parental allocation of food to nestling tree swallows: The influence of nestling behavior, sex, and paternity. *Animal Behaviour*, 65, 1203–1210. doi:10.1006/anbe.2003.2178
- Wilcox, A. J. (2001). On the importance—and the unimportance—of birthweight. *International Journal of Epidemiology*, 30, 1233–1241. doi:10.1093/ije/30.6.1233
- Wilkins, J. F. (Ed.). (2008). *Genomic imprinting: Advances in experimental medicine and biology* (Vol. 626). New York, NY: Springer Science.
- Wilkins, J. F., & Haig, D. (2003). What good is genomic imprinting: The function of parent-specific gene expression. *Nature Reviews Genetics*, 4, 359–368. doi:10.1038/nrg1062
- Williams, G. C. (1966). *Adaptation and natural selection: A critique of some current evolutionary thought*. Princeton, NJ: Princeton University Press.
- Wilson, M. I., Daly, M., & Weghorst, S. J. (1980). Household composition and the risk of child abuse and neglect. *Journal of Biosocial Science*, 12, 333–340. doi:10.1017/S0021932000012876
- Zahavi, A., & Zahavi, A. (1997). *The handicap principle: A missing piece of Darwin's puzzle*. New York, NY: Oxford University Press.
- Zhao, Q., Tan, C. L., & Pan, W. (2008). Weaning age, infant care, and behavioral development in *Trachypithecus leucocephalus*. *International Journal of Primatology*, 29, 583–591. doi:10.1007/s10764-008-9255-8

Received September 23, 2010

Revision received April 13, 2011

Accepted April 13, 2011 ■