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## Parental Investment Theory (Middle-Level Theory in Evolutionary Psychology)

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### Synonyms

[Parental care, parenting; Resource provision](#)

### Definition

*Parental investment* is referred to as any expenditure (time, energy, resources, etc.) that a parent incurs to benefit an offspring. *Parental investment theories* in evolutionary biology and evolutionary psychology explore mechanisms underlying parent-offspring relationships and investment. These theories examine adaptive functions and fitness dynamics of parent-offspring relationship, and how environmental conditions, sex differences in provision of reproductive resources regulate parental investment in sons and daughters.

### Introduction

Throughout hominid evolution, our ancestors have always managed to do two things: survive

to reproductive age and reproduce. Human survival and reproduction are characterized by internal fertilization, long-term gestation, lactation, and prolonged infancy that requires intense parental care and investment. *Parental investment*, in evolutionary biology and evolutionary psychology, is referred to as any expenditure (time, energy, resources, etc.) that a parent incurs to benefit an offspring (Trivers 1972).

From an evolutionary perspective, offspring are genetic vehicles for their parents. Without children, an individual's genes would perish. It is thus reasonable to expect that natural selection would favor powerful mechanisms in parents that ensure the survival and reproductive success of their children. Parental investment is thus pivotal for both offspring survival and perpetual reproductive success of the parents. Parental investment is viewed as a cost in parental fitness, via either direct physical or physiological expenditure or indirect opportunity cost in mating and reproduction.

### Fisher's Principle

A pioneering analysis of parental investment can be traced back to Ronald Fisher. In his 1930 book *The Genetical Theory of Natural Selection*, Fisher developed an evolutionary model to explain why the sex ratio of most species that produce offspring through sexual reproduction is approximately 1:1 between males and females.

Fisher's model suggests that parental investment should also covary with this dynamic of evolutionary equilibrium. Fisher built his argument in terms of parental expenditure and predicted that parental expenditure may deviate from the 1:1 ratio but would be "corrected" back to an equal distribution by natural selection. Suppose females outnumber males in a population due to a war situation. A newborn male then receives more parental investment and would have better mating prospects than a newborn female and therefore can expect to have more offspring. Therefore, parents who are genetically more disposed to producing males would have more than average numbers of offspring. As a result, male to female sex ratio becomes higher than 1:1. The demand and supply relationship thus is changed and then reversed: the shortage of males is replaced by a shortage of females. The male to female sex ratio is then downregulated toward the 1:1 equilibrium. Similarly, in situations that female births are less common than male births, the sex ratio would be regulated down toward the equilibrium (Hamilton 1967).

Regulated by natural selection, the total parental investment incurred will be equal across sex for children. This implication from Fisher's principle stands in contrast to persistent differential parental investment in sons and daughters. One way to understand the coexistence of the 1:1 sex ratio and differential parental investment is to view the former as population equilibrium and the latter as individual strategies that are dependent upon situational factors and the life-stage of the parents.

Sex ratio of an entire population is not as sensitive as operational sex ratio to natural selection and sexual selection. *Operational sex ratio* is a measure that is more sensitive to sexual selection. It is the ratio of sexually competing males that are ready to mate to sexually competing females that are ready to mate (Clutton-Brock 2007). This is a measure of how intense sexual competition is in a population and the potential rate of reproduction. This ratio reflects the severity of intrasexual mating competition and is controlled by relative parental investment (Gwynne 1990). For example, if females spend more time

caring for young than mating, but males do the opposite, then more males would be ready to mate, thus creating a male-biased operational sex ratio.

### Hamilton's Inclusive Fitness (Kin Selection) Theory

Parental investment theory can be viewed as a branch of kin selection theory. Building upon Fisher's (1930) work, W. D. Hamilton (1964) proposed his inclusive fitness theory, which argues that altruistic acts toward neighbors who have copies of the helper genes would be favored by natural selection. Inclusive fitness theory holds the keys to understanding differential investment behaviors, including parental investment. The mathematical treatment of the theory ( $C \leq rB$ ) is now often referred to as Hamilton's rule, which shows that an "altruistic design" can spread through the population if it causes an individual to help a kin member whenever the cost ( $C$ ) to the helper's own reproduction is offset by the benefit ( $B$ ) to the recipient's reproduction, weighted by the genetic relatedness between the two ( $r$ ).

Hamilton's (1964) inclusive selection theory has been a powerful source for generating hypotheses about altruistic behaviors in social interactions, for which standard economic models fail to account. Hamilton (1964, p. 19) predicted that: "The social behavior of a species evolves in such a way that in each distinct behavior-evoking situation the individual will seem to value his neighbor's fitness against his own according to the coefficients of relationship appropriate to that situation." For kin selection to work, a prerequisite is that "a suitable social object is available" in an interactive social context (Hamilton 1987, p. 420). Parent-offspring interaction thus might be the most typical case for kin selection.

Hamilton's rule also suggests *extended forms of parenting* from kin who are not biological parents. For example, Gorrell et al. (2010) showed that surrogate mothers of red squirrels adopt related orphaned squirrel pups but not unrelated orphans. The authors of this study calculated the cost of adoption by measuring a decrease in the

survival probability of the entire litter after increasing the litter by one pup and the benefit of adoption as the increased chance of survival of the orphan. More precisely, females adopted orphans when  $rB > C$  but never adopted when  $rB < C$ .

Another form of extended parenting can be seen in *eusociality* (true sociality) which is characterized by overlapping generations between parents and their offspring, cooperative brood care, and the specialized castes of nonreproductive individuals (Freeman and Herron 2007). Social insects provide good examples of extended parenting. The workers of some species are sterile, a trait that would not occur if individual selection was the only process at work. The relatedness coefficient  $r$  is abnormally high between the worker sisters due to *haplodiploidy*, whereby males are haploid and females are diploid. This ensures that sisters are more related to each other than they ever would be to their own offspring. Hamilton's rule readily accounts for such extended parenting behavior, though there are alternative explanations (see Nowak et al. 2010).

Humans also exhibit extended forms of parenting. A study of childcare practices among Canadian women found that respondents with children provide childcare reciprocally with nonkin. The cost of caring for nonkin was balanced by the benefit a woman received – having her own offspring cared for in return. However, for individuals without their own offspring, the inclusive fitness benefits of providing care to closely related children might outweigh the time and energy costs of childcare. Indeed, the respondents without children were significantly more likely to offer childcare to kin only (Davis and Daly 1997).

### Trivers' Model of Parental Investment

Inspired by seminal work of Hamilton (1964), Robert Trivers, then a graduate student at Harvard University, developed a theory of parental investment as a result of sexual selection. In *iteroparous* species, where individuals may go through several reproductive bouts during their lifetime, a tradeoff may exist between investment in current

offspring and future reproduction. The importance of parental investment can be seen especially in species in which the offspring are altricial (i.e., unable to fend for themselves from earliest ages). In many bird species and in modern humans, this leads to males spending more time caring for their offspring than do the male parents of precocial species, since reproductive success would otherwise suffer.

Based on this cost–benefit analysis, Trivers (1972) defined the term parental investment to mean 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. Overall, parents maximize the difference between the benefits and the costs, and parental care will be likely to evolve when the benefits exceed the costs.

The evolution of sex differences in parental investment is widely attributed to anisogamy (i.e., sexual reproduction involving two types of gametes that differ in size). The initial asymmetry in premating parental investment (eggs vs. sperm) is assumed to promote even greater divergence in postmating parental investment (parental care). In such a situation, a male's reproductive success is limited by his ability to fertilize eggs with his sperm in the same-sex mating competition. A female's reproductive success is limited by her ability to produce eggs, which requires a large investment of metabolic energy (Trivers 1972, p. 138).

In humans, parental investment starts from the point when the sperm fertilizes the egg. Following fertilization, the minimal obligatory parental investment for the female is 9 months of pregnancy, followed by delivery. In contrast, the minimal obligatory parental investment for the male is almost zero. This difference of minimal obligatory investment between males and females suggests that the amount of investment and effort put into mating and parenting would also differ.

Trivers (1972) introduced two arguments to link premating and postmating investment. The first argument is that females are more committed than males to providing care because they stand to lose a greater initial investment. The second

argument takes the reasonable premise that anisogamy produces a male-biased operational sex ratio leading to males competing for mates. Male care is then predicted to be less likely to evolve as it consumes resources that could otherwise be used to increase competitiveness.

These two arguments however are challenged by other scholars (see Kokko and Jennions 2008). The first argument has been criticized for committing the “Concorde fallacy” as optimal decisions should depend on future payoffs, rather than past costs. However, the argument can be made in terms of residual reproductive value when past investment affects future payoffs. The second argument was challenged by the Fisher principle. Given each offspring has precisely two genetic parents, a biased operational sex ratio would generate frequency-dependent selection that favors increased parental investment by the sex facing more intense competition, in this case males.

Although facing some theoretical challenges, predictions from Trivers’ (1972) model received ample empirical support. Using measures from time spent in vicinity, touching, and teaching children shows that women indeed care for their children more intensively than men do (Geary 2000).

Besides the mating opportunity costs hypothesis suggested above, another mechanism underlying the phenomenon that mothers invest more than fathers in offspring is the *paternity uncertainty* hypothesis. Mothers, consciously or not, are “sure” of their genetic contribution to their offspring (maternity certainty). When a female gives birth or lays a fertilized egg, there is no doubt that her offspring will contain 50 % of her genes. In contrast, from a male’s perspective, there can always be some probability that the offspring was fathered by another male (paternity uncertainty).

## Parent-Offspring Conflict

Given the importance of offspring, one of the astonishing facts about parental care is that many species do not engage in it at all (Alcock 2001). Part of the reason for the lack of universality of parental care is that it is so costly. By investing in

offspring, parents lose out on resources that could be devoted to themselves or toward finding additional mates. Parents who protect their young risk their own survival. Thus, when fitness cost is higher than fitness benefit, a stopping mechanism becomes necessary.

From an evolutionary perspective, parents and children are predicted to have conflicts. Following his own work on parental investment and sexual selection, Trivers (1974) developed a model of parent-offspring conflict. In sexually reproducing species such as humans, parents and offspring are genetically related by 50 %. This genetic relatedness between parent and child can exert selection pressure for parental care. But it also means that parents and children differ genetically by 50 %. Fitness benefit for one is not perfectly correlated with fitness benefit for the other. Specifically, parents and children will diverge in the ideal allocation of the parents’ resources, the typical result being that children want more for themselves than parents want to give (Trivers 1974).

For a parent of two offspring with two units of food available, the optimal allocation would be to give one unit of food to each offspring. Considering that there is a diminishing return associated with each additional consumption, the value of the first unit of food consumed is higher than the value of the second unit of food. However, for each offspring, the ideal allocation is to get two units of food. The theory of parent-offspring conflict predicts that each child will generally desire a larger portion of the parents’ resources than the parents want to give. In addition, parent-child conflict over the parents’ resources is predicted to occur not merely at particular times such as adolescence, but at each stage of life.

Trivers’ theory (1974) identified an important area of genetic conflict of interest between parents and children. Over evolutionary time, there will be an “arms race” between the genes expressed in parents and the genes expressed in children. Selection is therefore predicted to forge adaptations in children to manipulate parents toward the children’s optimum resource allocation and counter-adaptations in parents to manage resource allocation toward their own optimum. This theory yields some surprising predictions. For example,

mother-offspring conflict will sometimes occur in utero, such as over the blood supply to the fetus, the size of the fetus, and whether the fetus is spontaneously aborted. Empirical evidence supports these predictions (Haig 1993).

### **r/K Selection Hypothesis and Life-History Theory**

The other overarching theory that is closely relevant to parental investment is the r/K selection theory by MacArthur and Wilson (1967). According to the theory, when resources are sufficient to carry or support organisms living in an environment, organisms would be able to freely exploit rich resources for fast development and early reproduction that is characterized by a large number of offspring with little parental investment. This is known as r selection, with r representing the maximal reproductive rate of a species. In contrast, when resources become scarce, organisms adopt slow strategies, also known as K selection, with K representing the carrying capacity of the environment. K selection favors slow development and intense parental care and investment to reproduce few, high-quality offspring who can compete for and monopolize the depleting resources of the environment.

Species with K-selected traits, such as large body size, long life expectancy, and the production of fewer offspring, which often require extensive parental care until they mature, include elephants, humans, and whales. Although some organisms are identified as primarily r- or K-strategists, the majority of organisms do not follow this pattern (Hrdy 2000). The r/K dichotomy can be expressed as a continuous spectrum using the economic concept of discounted future returns, with r-selection corresponding to large discount rates and K-selection corresponding to small discount rates (Reluga et al. 2009).

The r/K selection theory has been challenged by its lack of empirical support and led to a newer paradigm of life-history theory that focuses on age-specific strategies and incorporates many of

the themes important to the r-K paradigm (Reznick et al. 2002).

Life-history theory provides an evolutionary and psychobiological framework for studying parental investment. The theory primarily concerns tradeoffs among various survival and reproductive needs given finite energy and resources and infinite inter- and intra-species competition (Stearns 1992). The most essential tradeoffs are between somatic effort (growth, learning, and socialization) and reproductive effort. Reproductive effort itself involves the additional tradeoff between mating effort that results in offspring quantity and parenting effort related to offspring quality.

Calibrated in terms of fitness or reproductive success, all tradeoffs can be summarized as the tradeoff between current or early reproduction and future or delayed reproduction. Varying along the fast-slow continuum, differences in life-history strategies result in the vast individual differences in observed behavior (Del Giudice and Belsky 2010). Variations in life-history strategies are the result of environmental conditions. Two overarching conditions relevant to life-history strategies are the extent of environmental harshness and unpredictability regarding mortality and mobility. High levels of extrinsic mortality and mobility lead to the adoption of fast life-history strategies with low parental investment because fitness is maximized by accelerating development and initiating early reproduction before extrinsic mortality or mobility hits. Conversely, low levels of environmental harshness and unpredictability do not necessarily predict slow life-history strategies but depend on other factors in the environment, such as resource levels and the extent of intraspecific competition over resources (Ellis et al. 2009). The most effective forms of signals in a child's environment are parental behavior and related information, such as the absence or change of parental figures (Ellis 2004). The mere experience of changes in parental and other adult figures has been found to be a robust predictor of fast life-history strategies (Tither and Ellis 2008).

Studies of life-history strategies suggest that quality of parental investment affects the adoption of fast or slow strategies by the offspring, which in

turn determines the parental investment strategies of the offspring when s/he becomes a parent in the future.

## Differential Parental Investment in Sons and Daughters

### Trivers-Willard Hypothesis

Assuming an equal sex ratio in the population, sons and daughters, on average, have equal reproductive success. But the condition of the son or daughter might result in differential parental investment in sons versus daughters. This is the core insight of the Trivers-Willard hypothesis (1973). According to this hypothesis, rich parents are more likely to have successful offspring and should favor sons since there is a greater opportunity for their sons to be rich and to have more offspring. Conversely, poor parents should prefer daughters to sons because daughters are not as likely to be reproductively unsuccessful as sons.

Stated differently, if being in “good” condition affects male reproductive success more than female reproductive success, as we would expect in a polygynous mating system, then parents should bias investment toward sons if the parents are in good condition and toward daughters if the parents are in poor condition.

Tests of the Trivers-Willard hypothesis in humans have proved inconclusive (Keller et al. 2001). A few studies find a Trivers-Willard effect. In one study, for example, using years of education as a proxy for parental investment, Rosemary Hopcroft (2005) found that sons of high-status men attained more years of education than daughters, whereas daughters of low-status men reached higher education levels than sons. She also found that high-status men sire more sons. Future studies are needed to determine whether the hypothesized Trivers-Willard effects are found among different populations of humans. Gaulin and Robbins (1991) found support for the Trivers-Willard hypothesis in their study of North American women. However, additional tests of this hypothesis have produced mixed results, particularly with human samples. In a study with larger data sets, Keller et al. (2001) reported that

their results did not replicate the findings of Gaulin and Robbins (1991). Based on the analysis of the results from their own and other previous studies, these authors conclude that Trivers-Willard effects are at best tiny in the contemporary United States, where resources are too abundant compared to the typical conditions of hominid evolution.

### Reproductive Variance Hypothesis

An alternative account of differential investment in sons and daughters focuses on the reproductive variance of sons versus daughters. The concept of variance in reproductive payoffs has been pivotal in some recent evolutionary analyses of behavior (see, for example, Daly and Wilson 1997). The evolutionary logic for risk/variance sensitive strategies is that selection would favor a greater risk-proneness when risk avoidance promises not fitness but reproductive failure. Universally and throughout hominid evolution, men have a higher reproductive variance than women. That is, women tend to consistently produce a few children whereas men tend to have either a lot of offspring or zero offspring. From a Darwinian perspective, risks can be viewed as variance in reproductive fitness in terms of the number of offspring one has (Wang 2002). Thus, parental investment in daughters versus sons is like a risky choice between a safer bet and a gamble (a more probabilistic bet), respectively.

Following this line of thinking, parents from a contemporary US population whose wealth conditions are not clearly diversified tend to have comparable parental expectations (aspirations) for their children’s financial and reproductive prospects. Thus, what affects their differential investment in sons or daughters would be their psychologically perceived relative wealth compared to their neighbors instead of absolute wealth. When the perceived relative wealth is lower, the distance to parental expectations would be higher. Thus, sons would be favored since a higher variance in sons’ financial and reproductive success would increase the chance of reaching the parental expectations or goals. Conversely, daughters would be favored by parents who have a higher perceived wealth.



Therefore, a reversed Trivers-Willard effect is likely to be found in a less stratified population as a result of the difference in perceived relative wealth. In contrast, a Trivers-Willard's effect would be more likely to be found in a population with a stratified wealth structure. For instance, if a wealthy parent has a much higher than average expectation for his or her children's financial and reproductive success, sons would be favored, thus a Trivers-Willard's effect.

In a field study conducted in villages in north-west China, Wang (2002) found a reversed Trivers-Willard's effect when perceived wealth condition (rated on a 1–9 scale against families in the same local area) was taken into account. The interbirth interval as a measure of parental investment was significantly longer after having a son than after having a daughter for the families with lower perceived wealth but not the families with higher perceived wealth.

In another field study conducted in a Midwest U.S. rural community where the wealth structure was also unstratified, Wang (2007) found that actual household income affected overall parental investment in a child irrespective of the sex of the child, using breastfeeding and interbirth interval as the measurements of the degree of parental investment. In contrast, perceived wealth by parents relative to their neighborhood households affected differential investment in sons versus daughters. Independent of real income of the family, IBI was longer if the parents' perceived family wealth was lower. This effect of perceived wealth on IBI was evident both for daughters and sons. As predicted from sex-specific reproductive variance, a differential breastfeeding pattern in sons and daughters emerged. In the families of higher perceived wealth, the average percent of daughters being breast fed was significantly higher than that of sons (67 % vs. 36 %). In contrast, in the families of lower perceived wealth, the percent of daughters being breast fed decreased to 52 % and the percent of sons being breast fed increased to 49 % percent.

The results from these two studies suggest that investing in sons is riskier than investing in daughters. In terms of parental economics, sons can be viewed as a riskier prospect than daughters

since men, on average, have a higher variance in wealth and reproduction than women.

## Conclusion

Parental investment theories in evolutionary biology and evolutionary psychology have provided overarching frameworks and testable mechanisms that lead to novel predictions about parent-offspring relationships and investment. *Fisher's model* focuses on the natural selection mechanism that maintains the 1:1 equilibrium in sex ratio and how parental investment covaries with the dynamic of the equilibrium. *Hamilton's inclusive fitness model* reveals the production rules for the evolution of cooperation between kin, including boundary conditions for parental investment. *Trivers' model* identifies a link between parental behavior and sexual selection, and sex-specific differences in reproductive resource provision before mating and post-reproduction. Since that parental investment is costly for the parents and that the genetic relatedness of a child to either of the parents is 50 %, the ideal resource allocation for a child does not coincide with the ideal resource allocation for the parents. Thus, parent-offspring conflict is inevitable and ubiquitous. *Parent-offspring conflict theory* thus provides unique predictions for parental investment related behaviors. The *r/K selection model* and *life-history theory* view parental investment as an adaptation to environmental harshness and unpredictability regarding mortality and mobility. Evolutionary analyses also help to understand *differential parental investment*. The concept of *paternity uncertainty* is used to account for one type of differential parental investment that mothers invest more in offspring than fathers. The *Travers-Willard hypothesis* predicts another type of differential investment in sons versus daughters by the parents, contingent upon the wealth condition of the parents. An evolutionary analysis based upon *reproductive variance* in sons versus daughters offers an alternative mechanism for understanding differential parental investment.

## Cross-References

- ▶ [Evolution of Cooperation](#)
- ▶ [Genetic Relatedness Affects Aid to Kin](#)
- ▶ [Hamilton's Rule and Theoretical Implications](#)
- ▶ [Kin Selection](#)
- ▶ [Life History Theory](#)
- ▶ [Operational Sex Ratio](#)
- ▶ [Parent-Offspring Conflict \(Trivers\)](#)
- ▶ [Paternity Uncertainty](#)
- ▶ [Reproductive Strategy](#)
- ▶ [Reproductive Value; Sex Ratio](#)

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