Differential infant mortality viewed from an evolutionary biological perspective

Jan Beise, Eckart Voland*

Center of Philosophy and Foundation of Science, Giessen University, Otto-Behaghel-Strasse 10c, Giessen D-35394, Germany

Abstract

Evidence from family reconstitution studies suggests that variations in infant mortality may reflect differences in parental solicitude. For various proximate reasons that might originate from emotional, material or social interests, parents may be inclined to invest differently in the survival of their offspring. Evolutionary theory holds that the behavior-regulating mechanisms that cause differential parental care operate in a biologically functional manner. They obey the biological imperative of striving to propagate one’s own genetic material in the gene pool of the population to the best possible degree, in view of prevailing socioecological constraints. From a Darwinian point of view, differential parental investment can be best understood as a socioecologically contingent tactical measure within an adaptive, i.e., genetic fitness enhancing strategy. Therefore, human reproductive decisions remain poorly understood unless their biological function in the Darwinian fitness competition is taken into consideration.

© 2002 Elsevier Science Inc. All rights reserved.

Keywords: Infant mortality; Differential parental care; Genetic fitness

1. Introduction

According to a Low German proverb, Leewe Kinner hebben vööl Namen (cherished children have many names). In fact, a count of the names in the baptismal register of the East Frisian parish of Reepsholt (1650–1700) revealed that, in farm families, sons and daughters...
who survived their first year had been given more godparents, on average, than siblings who died as infants (Voland, 1989). Although it is unlikely that infant survival was directly dependent on the number of godparents, their selection may well have reflected the parents’ joy or indifference toward the arrival of a new child and served as a proxy for parental interest and the extent and quality of infant care, specifically in terms of the duration of breast-feeding. Such differences in parental attention in the final analysis may have had a substantial impact on infant survival.

Indications of apparent discrimination against certain infants can be found in other evidence. In the East Frisian region of Krummhörn, northwest of Emden, the mortality rate of farmers’ sons was higher than that of laborers’ sons. They also suffered from excess infant mortality compared to their female siblings. Indeed, the extent of excess male mortality was significantly higher than might have been expected given the fact that newborn males, in general, are members of the constitutionally weaker sex (Voland, Siegelkow, & Engel, 1991). Another vernacular saying, *Ordnung regeert de Welt, un de Knuppel de Jungens* (order rules the world and the cudgel rules the boys), suggests that higher rates of male infant mortality in farm families in part may have been the result of parental choice. Krummhörn farmers had good reasons for desiring only a few sons: as a rule only the youngest son inherited, while other male siblings had to be compensated by the heir, thus undermining the economic viability of the family holding and causing its ruin under certain circumstances.

More conventional historians and social scientists could eventually classify this phenomenon as a manifestation of a specific cultural history. Sociobiologists and behavioral ecologists, with their concern for exploring adaptive behavior and its evolutionary origins, would use recent insights from evolutionary theory to explain such differences in parental care and infant mortality. In particular, the manner in which people manipulate the future of their families has deep biological roots and is not simply a result of cultural factors (Daly & Wilson, 1995). Many observers may be surprised by the idea that complex, differentiated human strategies can also be understood from a biological point of view, particularly as human behavior is embedded in a cultural context where decisions are influenced by emotions, rational choice or objective planning. However, within a Darwinian framework the proximate mechanisms that regulate human behavior, such as emotions, motivations, and cognition, are themselves the object of biological evolutionary theory. These mechanisms have evolved through a long process of biological adaptation, specifically because they were best able to translate the biological imperative into biologically functional behavior, or to use the technical jargon of biologists, because they maximized genetic fitness (Barkow, Cosmides, & Tooby, 1992; Betzig, 1997; Buss, 1999).

2. The evolutionary perspective

Behavioral ecologists of Darwinian orientation are not interested primarily in putting forward alternative interpretations of more conventional historical perspectives: instead, they seek to analyze observable behavior differently. Even if we can understand how the ecological, economic or cultural conditions of a specific population influence the treatment of children, and
indirectly infant survival, the question remains as to why the human psyche works in such a way. Why are humans as impressionable in their attitudes to children (and other reproductive decisions) as they obviously are? In other words, evolutionary biologists are concerned with exploring the ultimate causes of human behavioral variability and its evolution over time. Like all other organisms, humans are the product of evolution and are subject to the mechanisms of natural selection. Although theoretically unlimited, the reproductive potential of a population is confronted by limitations on resources such as food, hiding or breeding places, mates, and social support. Resources are important not only for an individual’s own growth, but also for raising offspring; limited resources automatically lead to competition between the members of a population. Individual variability with respect to the ability to secure and exploit these resources leads to differential reproduction. Better-adapted individuals are able to secure more extensive or useful resources and may have other capabilities that also have a positive effect on their survival and reproduction. They therefore leave behind more offspring than poorly adapted members of the same species. Thus, natural selection implies a type of assessment of the individual with respect to lifetime reproductive success. Traits that are subject to the process of adaptation because they influence survival and lifetime reproduction are not only morphological or physiological in nature, but also psychological.

Nevertheless, even if natural selection applies to the overall external appearance of the individual (the so-called phenotype), the gene is the ultimate unit of evolution, because the genes provide the code for the development of the phenotype. All developmental processes—whether with regard to physical or mental traits, or among animals and human beings—always occur in the interplay between genetic information and environmental factors. Genes merely define the reaction norm to the specific developmental context, as the environment always co-influences the development of the phenotype. A phenotype, therefore, is a manifestation of a genotype within the context of a very particular development.

In evolutionary history, there has been a permanent test, operated by natural selection, of which environmental characteristics contain useful information for successful individual development and which do not. Viewed in this manner, the sensitivity of an organism to its milieu, or the manner in which it allows itself to be influenced while growing or making reproductive decisions, is itself an outcome of the evolutionary process. Human behavior is inherently flexible, which means that to fulfill their purpose behavior-controlling mechanisms are extremely versatile and adaptable. The variability of complex behavioral patterns, such as how humans deal with their offspring, reflects, to a considerable degree, environmental variations. And it is specifically in this context that biological functionality can be observed. The specific mechanisms that translate environmental variations into behavioral variations are diverse. They can include the context-activation of specific genes (reactive genetics), the influence of environmental parameters on physiological processes, or a cognitive processing of one’s life situation. The critical factor in natural selection is whether the evolved mechanisms evoke the right behavior at the right time; the optimizing evolutionary behavior of all species in the long run indicates that this is generally the case. Humans are no exception, and the results are biologically functional behavioral strategies. In other words, throughout the evolutionary history of a species, genetic dispositions for all aspects of life, whether physical or mental, are automatically selected for optimal reproductive efficiency.
This includes all those physiological and mental mechanisms that are responsible for reproductive decisions, as they are constantly being made throughout an individual’s life span, the sum of which comprise a specific reproductive career or “life history.”

3. The evolution of reproductive strategies

Life history strategies are evolved to contribute genetic material to the following generations in the best possible way. They can be understood as the effort of the “selfish gene,” and depending on the life functions or targets in which investments are made, various forms of effort can be differentiated. Somatic effort represents the investments by an organism in its growth, development, and differentiation as well as its repair and maintenance, which enable it to accumulate reproductive potential. By contrast, reproductive effort focuses specifically on reproduction by exploiting the existing reproductive potential of an individual. Reproductive effort, in turn, assumes different forms: it may require time, energy, risks to life, social reputation, or material resources; it can occur in connection with sexual competition, the formation of gametes, embryonic development, and postnatal care for offspring. Reproductive effort also involves costs (Williams, 1966), which is why natural selection cannot favor unrestricted reproduction. Instead it optimizes the nature and manner in which reproductive effort is allocated to reward those measures that lead to the greatest net yield in reproductive fitness over the course of an organism’s life. Trade-off problems occur when two or more traits are limited by the shortage of the same resources (Borgerhoff Mulder, 1992; Hill, 1993; Stearns, 1992). As any unit of effort can only be invested once, evolution has shaped humans (and all other organisms) into reproductive strategists who constantly have to make decisions about the best possible allocation of their limited investment possibilities. Some of these allocation decisions have been genetically fixed in the organism’s phylogenies, but others require spontaneous adjustments to prevailing life circumstances.

In terms of potential allocation conflicts, four basic problems recur constantly: Firstly, should priority be given to somatic or reproductive effort by maximizing current or future reproduction? Should an organism continue to invest in itself, reinforce its physical or social quality and competitiveness, repair itself, and accumulate resources somatically or extra-somatically (as education or wealth) or should it begin to reproduce instead? Secondly, should priority be given to direct or indirect reproduction? Should an organism reproduce itself or support relatives in their reproduction by assuming, either temporarily or permanently, the role of helper-at-the-nest? Thirdly, a choice has to be made between mating and parental effort. For males, the trade-off is often between so-called “cad versus dad” strategy, whereas females can either continue to search for a better mate or terminate the search and begin reproduction. Fourthly, should a priority be established on the quality or quantity of offspring? With an increasing number of descendents, the amount of parental investment in each single offspring must be reduced accordingly. Thus an optimization problem may result with respect to lifetime fitness. Should one aim for a few, well-endowed offspring capable of surviving and competing or for many who are less able to cope with life?
Constraints on personal reproduction can vary greatly among individuals for many reasons, whether genetic, ecological, social or random. Consequently, individuals will seek different solutions to problems of allocation and, as a result, natural selection will not promote optimal allocation strategies, but the best that are available within given circumstances (McNamara & Houston, 1996). This is a strong argument for studying reproductive processes and decisions, both at the individual level and in relation to whole populations (Low, 1993; Voland, 2000).

4. Childcare strategies

Parental styles differ widely with regard to the value each individual child assumes in a family’s reproductive efforts. At one extreme are parents convinced that an offspring’s fate is subject to a series of unavoidable risks, while at the other are those who feel extremely responsible for what happens to their children. Individual attitudes are frequently rationalized by world views colored by religion, but parents, as a result, differ in terms of their efforts to provide the best possible nutritional, medical and mental hygiene for their offspring and in their attempts to protect them from the general risks of life. Moreover, as behavioral ecology predicts, parental responsibility for the life and death of children in some way reflects the experience of actual survival chances and are therefore nurtured ecologically. Indeed, social—historical research demonstrates the extent to which everyday experiences of the fragility of life have a deep and lasting impact on the mentality of a population and in the long run affect attitudes to children (Imhof, 1984). Persistent Malthusian checks, for example, whether as a result of war, hunger, or epidemics, will reinforce a predominantly fatalistic attitude to life and encourage a greater degree of parental indifference to the survival of their children. On the basis of life history theory, parental effort was dependent on adult mortality, which was the key factor that affected parental investment inclinations (Chisholm, 1993). The stronger the threat from extrinsic mortality risks (parasites, predators, resource instability, aggressive encounters), the lower per-capita investment in children would be. Conversely, priority would also be given to increasing fertility which, in turn, would contribute to higher infant mortality. Infant mortality rates, therefore, have an intrinsic component that can be described as avoidable deaths.

Parental childcare styles vary through adaptation not only in response to differences in extrinsic mortality, but also to other factors, including subsistence strategies and workload or the availability of alternative caretakers (Blurton Jones, 1993; Hewlett, 1991; Hurtado, Hill, Kaplan, & Hurtado, 1992; Panter-Brick, 1995; Turke, 1989). Depending on the socio-ecological situation, natural selection favors parental styles with different outcomes, including maximization of offspring production, their survival, or social and material endowment (Blurton Jones, 1993). However, individual children frequently have a different status in parental reproductive strategies: individual children may be more or less preferred within the same family and may be assigned markedly different roles. Indeed, parents have a broad range of possibilities in determining the differential treatment of offspring, whether in respect to intrauterine care of the embryo and fetus, the choice of abortion or infanticide rather than
upbringing, the nature of postnatal care (specifically the duration of breast-feeding and medical support), and the investment in education or material endowment through dowry or inheritance payments (Voland, 1998).

From the perspective of behavioral ecology, differences in the psychological desirability, care, and endowment of one’s offspring would be expected to have a biologically functional background. The relative level of investment in each individual child, in turn, depends on two factors: the relative costs of parental investment and the predicted benefits (Clutton-Brock, 1991). The adaptive value of a possible investment reflects the net balance between these factors. From a biological point of view, differential parental care is contingent on the opportunity structure of the individual socioecological context that can best fulfill the biological imperative of genetic reproduction.

5. Adaptive investment strategies: the Krummhörn case

Differential parental investment in 18th- and 19th-century Krummhörn can be taken as exemplifying the Darwinian hypothesis. The Krummhörn region covered an area of 153 km² (largely marshland) with a relatively stable population of about 14,000 residents in 32 parishes. The land, which had recently been drained, was extremely fertile in terms of agricultural production, specifically dairy farming: it represented 7.3% of the total area of the province of Hanover in the late 19th century, but accounted for over 22% of agricultural output (Meitzen, 1894). The area was dominated by large and medium holdings; the traditional subsistence economy had been replaced by a capital-intensive, market-oriented agriculture, and some families had become relatively prosperous. As a result, the ownership of land was transferred to the youngest son (ultimogeniture), with other siblings receiving compensation in the form of money or chattels.

The North Sea surrounds the area on three sides, with the fourth side enclosed by barely accessible moorland. It was settled comparatively early, cultivable land was fully allocated, and hardly any common or more marginal land was left for development. Strict limits were placed, therefore, on geographical expansion and population increases, and the number of farms remained practically unchanged for many years or even tended to decrease. In terms of animal ecology, it represented a saturated habitat in which only a limited number of breeding places were available. Social stratification was also clearly delineated, and the ownership of land, specifically the size of holding, determined social prestige, political influence, and community rights. The ownership of at least 25 Grasen (one Gras = ca. 0.37 ha) or the lease of 50 Grasen was a prerequisite for being entitled to vote or to hold political or church office. The lifestyles of prosperous farmers, as a result, differed markedly in all material respects from the broad mass of agricultural laborers.

Data from the parish registers were processed on the basis of a family reconstitution study, and information on the size of individual family holdings was obtained from tax lists. Thus, it was possible to access data on individuals and their descendants over the course of several generations; this information, in turn, provided a basis for exploring the pattern of genetic and social reproduction and for investigating its biological adaptability (Voland, 1995). An
analysis of infant mortality revealed several interesting correlations between a child’s sex, his or her family’s social group, and the number of surviving siblings of the same sex. In the case of large-scale farmers, the infant mortality of sons (1q = 0.172) was almost 50% higher than that of daughters (1q = 0.120). By contrast, infant mortality rates among the sons and daughters of landless families were practically identical (1q = 0.114, 1q = 0.110) (Voland & Dunbar, 1995). Male infant mortality for the 60 families richest in land (1q = 0.230), which represented the Krummhörrn’s property élite, was approximately twice as high as the population mean (Klindworth & Voland, 1995).

Moreover, the mortality risk for the sons of large-scale farmers increased in line with the number of surviving brothers (Fig. 1); with three or more surviving brothers, the infant mortality rate rose to over 20%, more than one-third higher than for sons without older male siblings. By contrast, the number of surviving male siblings was not a key factor in determining the mortality risk of sons from landless families. A similar picture was evident for female offspring: whereas the number of surviving sisters had hardly any influence on female infant mortality among landless families (Fig. 2), the situation was noticeably different for the daughters of wealthier peasants. The presence of one or two older sisters was associated with a higher survival chance, but the mortality risk was unusually high if there were three or more older siblings.

Physiological explanations for the existence of a differential infant mortality risk by social class or gender can probably be discounted. Strong grounds exist, however, for arguing that it was a result of parental manipulation. The proximate mechanisms that might explain the mortality differential include differences in the duration of breast-feeding, in maternal

![Figure 1](image_url)  
**Fig. 1.** Male infant mortality (excluding stillbirths) according to the number of surviving brothers at an infant’s birth (Krummhörrn, Ostfriesland, 1720–1874). Source: Voland and Dunbar (1995).
responsiveness to a child’s needs, in mental-hygienic care, in the provision of nutritional and medical resources, as well as in other intra-familial transactions affecting the overall mortality risk in the face of latent threats to life, even if they do not appear to be particularly grave.

6. Opportunities for marriage and survival probability

If differential infant mortality can be traced back to differences in parental investment, it would indicate that every additional son—over and above the surviving male offspring—was of less value to the parents or even posed a threat. Both factors were evident to some extent in the Krummhörn region, primarily because of the economic displacement competition in which large-scale farmers engaged. During the 18th century, the number of large holdings fell slightly, agricultural land was concentrated in the hands of fewer farmers, and competition grew: tight limits were therefore imposed on the reproductive opportunities of the farming communities. To remain competitive, both economically and ultimately reproductively, the peasants had to avoid dividing the family holding at all costs. In the context of almost zero demographic growth, statistically every farming family was only able to produce two children to perpetuate its privileged social status: a son to take over the farm and a daughter to be married off to a family with equivalent socioeconomic standing. Every extra child would necessarily experience downward social mobility.

Moreover, too many sons represented a threat to the economic continuity of the farm: they had to be compensated by the inheriting brother even though any transfer of capital crucially weakened the economic viability of the family holding. These rules did not apply to
daughters to the same degree. According to East Frisian inheritance customs, which can be traced back into the Middle Ages, the value of a daughter’s settlement was only half that of a male sibling. This, in turn, provides an explanation for the registered differences in mortality risk, as the “production costs” of a daughter in terms of inheritance rights were significantly lower than those of a son. Accordingly, an overproduction of sons was more expensive for peasants with large holdings than an overproduction of daughters. This circumstance was also reflected in the marriage opportunities of children. Whereas the number of same-sex siblings had no significant effect on the marriage probability of children from landless families, the marriage opportunity for all children from large-scale holdings fell rapidly with an increase in the number of brothers and sisters who attained adulthood (Figs. 3 and 4). By contrast, parental manipulation was superfluous in the case of landless families, as there was no need to preserve the ownership of land by economic calculations or reproductive strategy. There were no obvious benefits or disadvantages for the families of agricultural workers in having a certain combination of children in terms of their number and sex, and they were therefore able to afford them a similar amount degree of parental care and affection (Figs. 3 and 4).

Fig. 3. Marriage probability for a 15-year-old boy according to the number of surviving brothers (Krummhörn, Ostfriesland, 1720–1874). Source: Voland and Dunbar (1995).

Fig. 4. Marriage probability for a 15-year-old girl according to the number of surviving sisters (Krummhörn, Ostfriesland, 1720–1874). Source: Voland and Dunbar (1995).
7. Differential parental investment as cost–benefit-oriented behavior

Differential parental investment can be understood as a cost–benefit calculation in two ways. Firstly, it was undertaken in the light of economic considerations, as the transfer of property from one generation to the next was taken into account when planning a family. To maintain the economic profitability of large-scale holdings, the withdrawal of working capital was consciously limited by minimizing the payment of legacies to non-inheriting siblings and by maximizing wealth concentration. This was achieved by an under-investment in surplus sons, in terms of parental care, which accounted for their lower survival rates in infancy. Since the production costs of daughters in terms of inheritance rights were noticeably lower, they could be absorbed more easily.

Secondly, differential parental investment on the part of large-scale farmers can also be interpreted as a cost–benefit calculation in terms of maximizing genetic fitness. The objective of maintaining the farm’s profitability also ensured the long-term survival of the family lineage and thus an individual’s own genes. The Krummhörn data indicate that economic success was correlated with long-term reproductive success (see Fig. 5), confirming the results from other investigations (Betzig, 1997); a married couple with a large-scale holding had almost twice as many descendants in the local population a century after their marriage as an average family had (Voland, 1990). Moreover, the probability of a married man dying without leaving behind at least one child who had attained the age of 15 years (i.e., the probability of total lineage extinction) varied significantly between social groups. The

Fig. 5. The average reproductive success of a married couple from the group of large-scale farmers in comparison with the standardized population for the first 100 years after marriage (Krummhörn, Ostfriesland, 1720–1750). Source: Voland (1990).
average risk was 12.5%, but only 3.3% for large-scale farmers (Klindworth & Voland, 1995). For the latter group in rural society, a balance had to be drawn between economic and genetic production. If families with large-scale farms wanted to maximize genetic success, they could not afford to jeopardize their economic success. This, in turn, could only be achieved through careful family planning, which in the 18th and 19th centuries meant active intervention in their children’s survival probability by precisely tuning the amount of parental care in relation to the expected benefits or costs of the concerned child.

8. Conclusion

Differential parental care, in specific circumstances, is the result of tension generated between reproductive interests and ecological and economic constraints. Sociobiology takes both factors into consideration in analyzing the extent to which natural selection has shaped our behavior-regulating machinery and the flexible solutions that are adopted in response to particular situations. One outcome of the behavior-regulating machinery is parental love that is conditional and strategic, given the objective of achieving the maximum efficiency of reproductive effort. It allocates care and attention in accordance with the opportunity structure for personal reproduction. Although it may appear paradoxical, sincere parental solicitude, child neglect, infanticide, and abortion are all manifestations of the same conditional parental strategy that serve the biological imperative. As active mechanisms of behavioral control, the emotions involved—love, affection, indifference, and hatred—directly regulate our social tendencies but in turn are regulated by profound reproductive interests (Frank, 1988; Wright, 1994). They can only serve to explain human behavior in a limited sense, given that motherly love (or the lack thereof) is more likely to be a consequence of an interest (or disinterest) in the child, rather than its cause.

References