

## CHAPTER 2

### **BIRTH ORDER, SIBLING COMPETITION, AND HUMAN BEHAVIOR**

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*Abstract:* Sibling competition is widespread among bird and animal species and sometimes leads to siblicide. By influencing the strategies that siblings employ in their struggles for dominance, birth order affects the outcomes of such contests. In our own species, birth order is a proxy for disparities in age, physical size, and status, all of which contribute to personality. In addition, birth order is related to the roles and niches available to offspring within the family system. On average, firstborns—who tend to act as surrogate parents—are more conscientious than laterborns, whereas laterborns are more agreeable, extraverted, and nonconforming. As strategies for dealing with rivals in a dominance hierarchy, as well as for optimizing parental investment, these sibling differences are consistent with a Darwinian perspective on family life. So are other links between personality and family dynamics, particularly those associated with parental investment and parent-offspring conflict. In adulthood, human behavior continues to reflect these formative influences, although such behavioral dispositions generally need to be catalyzed by appropriate situations in order to be fully expressed.

#### **1. THE BIOLOGY OF SIBLING COMPETITION**

A wide variety of animal species exhibit birth-order differences in behavior, usually in competition for parental investment. These behavioral effects are influenced by two distinct kinds of biological causes: *ultimate* and *proximate*. Ultimate causes include adaptive tendencies that have evolved by natural selection. Proximate causes comprise influences operating during the lifetime of the organism and encom-

pass biological as well as environmental factors, which almost always interact with one another. For example, some avian species possess an instinct to migrate during the autumn and spring, an adaptation that has its ultimate cause in natural selection. Temperature and day length, along with the various neuropsychological mechanisms they trigger, supply the proximate causes of bird migration (Mayr, 1961).

Viewed in these conceptual terms, a biological propensity to engage in sibling rivalry is one of the ultimate causes of personality development. Darwin's theory of natural selection explains this part of the story, which focuses on the biological dispositions that most offspring have to compete for parental favor. As William Hamilton (1964) recognized, natural selection maximizes inclusive fitness. This form of Darwinian fitness can be defined as an organism's own reproductive success, together with its contribution to the reproductive success of close relatives, discounted according to their coefficient of relatedness. On average, siblings share half of their genes. Hamilton's theory asserts that siblings will compete for scarce resources whenever the benefits of doing so are greater than twice the costs. Competition for parental investment is the main cause of sibling rivalry.

From a Darwinian point of view, sibling competition and parent-offspring conflict are flip sides of the same coin. Parents are equally related to all of their offspring and generally favor equal sharing among them, whereas siblings usually prefer a bias in their own favor. Among animals, weaning conflicts are an example of such disagreements. At the time of weaning, offspring want parents to continue investing in them, and them alone, whereas parents are inclined to reserve additional investment for future offspring (Trivers, 1974).

Darwinian and Freudian theory supply contrasting explanations for parent-offspring conflict, as Daly and Wilson (1990) have pointed out. In Freudian theory, such conflicts have their origins in the child's desire for sexual access to the opposite-sex parent—an urge that constitutes the Oedipus complex. In Darwinian theory, sexual desires have nothing to do with these conflicts. Rather, siblings compete to optimize parental investment and hence to get out of childhood alive. Siblings may be inclined to harm their rivals for parental investment, but they have no Darwinian incentive to harm a parent—at least not for the reasons Freud himself envisioned.<sup>1</sup> As Daly and Wilson have argued, Freud systematically misinterpreted evidence for parent-offspring conflict—which is generally nonsexual in nature—to fit his theoretical expectations.<sup>2</sup>

### Siblicide

Fatal sibling competition has been documented in insects, fish, and mammals. Even plants exhibit competition that sometimes ends in siblicide. The Indian black plum tree (*Syzygium cuminii*) develops seeds having 25 to 30 ovules—all siblings. Only one ovule survives to become the pit of the mature fruit—usually the ovule that is fertilized first. This first-fertilized seed secretes a “death chemical” that prevents its siblings from being able to metabolize sucrose, causing them to starve to death (Krishnamurthy, Shaanker, & Ganeshaiah, 1997).

Among animals, sibling competition usually centers around parental investment. Among sea birds and predatory birds, siblicide is particularly common (Mock, Drummond, & Stinson, 1990; Mock & Parker, 1998). In some species, such as African black eagles (*Aquila verreauxi*), siblicide is “obligate”—occurring in almost every instance. The female of this species lays two eggs, and the first-hatched chick pecks its younger sibling to death during the first days of life. In one documented case, an elder chick delivered more than 1,500 pecks to its younger sibling during the latter’s three-day lifespan. “In all siblicidal species studied to date,” report Mock et al., “there is a striking tendency for the victim to be the youngest member of the brood” (1990, p. 445). It is noteworthy that avian parents never intervene when chicks are engaged in siblicidal aggression. The parents’ own genetic interests are generally best served by raising one healthy chick rather than two undernourished ones.

Among blue-footed boobies (*Sula nebouxii*), females lay two or even three eggs. Siblicide is conditional in this species, depending on the food supply, which is therefore a proximate cause of siblicide. Aggressive pecking of a younger chick by an elder begins when the elder’s body weight drops below 80 percent of normal. In experimental studies in which the necks of booby chicks have been taped to prevent them from ingesting food, aggression increases sharply and is especially pronounced in the elder chick (Drummond & García-Chavelas, 1989).

Hatching order in boobies is associated with learned behaviors. In one experimental study, junior chicks that had developed subordinate behaviors were removed from their nests and paired with smaller dominants from another nest. Size normally decides dominance in boobies. In this experiment, however, smaller chicks that had previously been seniors were successful in achieving dominance over larger but previously junior chicks. The superiority of the smaller senior chicks

owed itself to their refusal to submit when attacked, and by their generally being more capable fighters than chicks that had previously been subordinate (Drummond & Osorno, 1992).

Whether siblicide is conditional or unconditional is determined by various ecological considerations that have shaped the genetic predispositions of each species. Blue-footed boobies do not have fixed territories, and, when the food supply is plentiful, they can generally rear more than one chick in a year. By contrast, African black eagles occupy fixed territories and their young require unusually large amounts of food, circumstances that limit the parents' ability to raise more than one chick, even in a very good year.

Why do avian parents regularly lay more eggs than are needed in any given breeding season? Two adaptive benefits are associated with this practice. First, an additional chick represents an insurance policy, in case an older chick dies of disease or predation. In species in which siblicide is conditional, the parents' reproductive success is enhanced whenever the food supply allows them to raise more than one offspring. Blue-footed boobies, for example, sometimes successfully rear three chicks, and many birds of prey are able to fledge two offspring.

Even in species in which siblicide is absent, proximate-causal mechanisms often regulate sibling competition. Female canaries (*Serinus canaria*) lay four or five eggs, which hatch on different days. Compared with their earlier-hatched siblings, the later-hatched chicks are physically underdeveloped. By laying each successive egg with greater amounts of testosterone, female canaries even the competition. The fifth egg, for example, may receive twice as much testosterone as the first. Testosterone accelerates neural development and also makes chicks more pugnacious, allowing the later-hatched chicks to compete more effectively for food (Schwabl, 1996; Schwabl, Mock, & Gieg, 1997).

### **Specialized Adaptations for Sibling Competition**

Among species that exhibit intense sibling competition, specialized adaptations have sometimes evolved to enhance the individual's chances of survival. Such adaptations for sibling competition often include weaponry in the form of teeth and other sharp structures. Tadpoles of the spadefoot toad develop teeth with which they cannibalize their broodmates (Bragg, 1954). Piglets are born with eye teeth that they shed after having competed for the sow's most nourishing teats. The earliest-born piglets head directly for the anterior teats,

which are richest in milk supply, and they fiercely defend these teats against encroachment by laterborn piglets. Compared with firstborn piglets, piglets born in the latter half of the litter are twice as likely to die before the third week (Trivers, 1985, p. 23).

Another striking case of adaptation for sibling competition involves spotted hyenas (*Crocuta crocuta*). Sibling competition begins as soon as the second pup is born, and fighting has been observed while the younger pup is still encased in its amniotic sac. Unlike other carnivores, hyena pups are born with fully erupted teeth, which assist them in these brutal struggles. Among spotted hyenas, 25 percent of offspring succumb to sibling aggression. In same-sex litters, the mortality rate is 50 percent. One explanation for this difference in mortality rates draws on theories about adult competition over reproduction (Hamilton, 1967). Female hyenas compete for the right to reproduce, and offspring generally acquire the rank of their mothers. Killing a sister eliminates a close-ranking competitor (Frank, Glickman, & Licht, 1991). This hypothesis works less well for siblicide among males, who disperse in early adulthood, so one must be cautious about endorsing an adaptationist interpretation for both sexes. Still, juvenile males face the task of integrating themselves into a new clan, and physical size is positively correlated with rank and reproductive success. Singleton pups experience greater rapid weight gain during the first year of life. As adults, they may also enjoy a reproductive advantage in competition with other males.

Evolution sometimes leads to specialized adaptations promoting sibling cooperation. In the Taiwanese aphid (*Pseudoregma alexanderi*), offspring exist in two forms, one of which is a soldier caste that defends the other caste from attack. Because members of this soldier caste remain in the first larval stage, they do not reproduce (Trivers, 1985, p. 42). Such morphological adaptations for altruistic behavior are explained by Hamilton's theory of kin selection. Because Taiwanese aphids reproduce parthenogenetically, offspring carry the same genes. The soldier caste's genes are therefore passed on by their reproductively active twins.

Hamilton's theory was prompted by his own study of another particularly altruistic insect group, namely, the social insects. Owing to the unusual genetic system of these species—called haplodiploidy—females are more closely related to their sisters (by  $3/4$ ) than they are either to their brothers (by  $1/4$ ) or to their own offspring (by  $1/2$ ). The unusually cooperative nature of social insect societies revolves around the fact that sisters, who do most of the work, suppress their repro-

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