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COOPERATION AND CONFLICT IN THE HUMAN FAMILY

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Dedication

To my parents, Yong-Ki Jeon and Young-Sook Park

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COOPERATION AND CONFLICT IN THE HUMAN FAMILY

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Despite the crucial importance of Hamilton's (1964) kin selection theory in evolutionary behavioral biology, psychological studies of family relationships have been relatively slow to incorporate a Darwinian perspective. One practical reason may be that existing evolutionary models of animal families, such as the honest signaling models, are applicable only if all family members fall into the same class in terms of age, sex, or health. The animal models are thus of limited use for investigating human families, in which the relative age of the child, as a corollary of birth order, may have played a pivotal role in shaping evolved family psychology. My dissertation has two main objectives: 1) to construct evolutionary mathematical models of family interactions that fully take into account the role of reproductive value and hence can be directly applied to human families; 2) to characterize the design features of evolved psychological mechanisms of human kinship by empirically testing *a priori* predictions derived from the models. I first examine how parents are expected to allocate their limited resources among offspring of differing ages. I show that the optimal strategy that serves parental interests is to bias parental resources toward the older offspring (chapter 2). I then empirically test the predictions derived from the first study, in comparison with previous evolutionary hypotheses of parental favoritism. The empirical results confirmed the predictions derived from the first study: in hypothetical allocation

tasks, participants allocated more tangible resources toward older children (chapter 3). Next, I investigate how intrafamilial conflict over the allocation of parental resources occur when each family member (a parent, its senior offspring, and its junior offspring) are allowed to differ in age. The results gained in this study may require a substantial revision of Trivers' (1974) classical theory of parent-offspring conflict. Moreover, it will open a fruitful avenue for inferring the adaptive design of psychological mechanisms dealing with sibling relationships (chapter 4). I then show that evolutionary insights can be also applied to the psychological study of distant kin relationships such as cousins (chapter 5).

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Chapter 1: Introduction

As the idiom “blood is thicker than water” implies, people generally agree that family relationships are more important than any other relationships. Family relationships, however, have been largely ignored by personality and social psychology. The textbooks of social psychology are overwhelmingly devoted to studies of stranger interactions. Even the subfield concerned with close relationships mainly focuses on mates and friends, not on blood kin (Daly, Salmon, & Wilson, 1997). Of course, the temporal development of kin relationships over the life-span has been actively investigated by developmental psychology. Yet the field fails to answer how various relationships among family members could be parsimoniously analyzed under a unified theoretical framework, let alone how they should develop over time (Buss, 2004).

By contrast, kin interactions have been the central focus of evolutionary biologists since Hamilton’s (1964) theory of inclusive fitness. Behavioral ecological study of animal sociality has now achieved a great success in providing powerful theoretical models and garnering plentiful empirical support. This dissertation is based on the conviction that modern evolutionary insights into social cooperation and conflict will revolutionize psychological research on human family systems. The contention is not new, being articulated more than 30 years ago (Alexander, 1979; Hamilton, 1975; Trivers, 1974; Williams, 1966; Wilson, 1975). Despite recent advances of evolutionary social psychology and evolutionary developmental psychology (Bjorklund & Pellegrini, 2002; Simpson & Kenrick, 1997), however, the evolutionary perspective has thus far inspired relatively little research on human kinship psychology (e.g., in contrast to human mating). I suggest that it is primarily because current intrafamilial interaction models in evolutionary biology have been based on a somewhat simplistic assumption that all offspring are identical in their ability to survive and reproduce. The assumption is reasonable when all offspring can be treated equally in some important respects (e.g.,

synchronously hatching birds where all offspring are of the same age). However, in many species including humans, the assumption is rarely justified, which makes it difficult for human psychologists to derive clear and testable predictions from evolutionary models.

My dissertation aims 1) to construct an evolutionary mathematical model of the family that can be directly applied to human family systems and 2) to characterize the design features of evolved psychological mechanisms of human kinship by empirically testing *a priori* predictions derived from the model. Specifically, I examine how intrafamilial conflict and cooperation are delineated within the human family, in which the genetic interests of parent(s), senior siblings, and junior siblings must diverge. Below I first briefly review the general theory of social evolution with an emphasis on intrafamilial conflict. I then discuss why it is necessary to construct an evolutionary model of the human family.

EVOLUTION OF SOCIALITY WITHIN THE FAMILY

Classification of social behavior

The theory of social evolution classifies social behaviors in terms of their effects on the reproductive success of the actor and on any recipient(s) (Hamilton, 1964; see Figure 1.1). First, *selfish* behaviors increase the fitness of the actor but decrease the fitness of the recipient. Second, *cooperative* behaviors increase both the fitness of the actor and the recipient. Third, *altruistic* behaviors decrease the fitness of the actor but increase that of the recipient. Lastly, *spiteful* behaviors decrease both. It should be noted that these four categories refer to the fitness effects of social traits, not to psychological states. According to Darwin's classical theory, altruistic and spiteful traits should not be favored by natural selection because they decrease the fitness of the individual bearing the traits and thus will fail to be passed on to the next generation. Altruistic behaviors,

however, are commonly found in nature and have been a serious problem for evolutionary biologists.

		Fitness effect on recipient	
		+	-
Fitness effect on actor	+	cooperation	selfishness
	-	altruism	spite

Figure 1.1 Hamilton's (1964) fourfold classification of social traits.

Hamilton's rule

It was Hamilton (1964) who solved the vexing problem. He emphasized that statistical associations between individuals will influence the course of natural selection. If an individual bearing genes encoding altruistic behavior is positively associated with other individuals carrying the same genes (e.g., through a common genealogy), then the altruistic individual will receive more altruistic acts from its social partners. Thus the fitness of an individual is affected not only by its own phenotype but also by the phenotype of its neighbors. This is called *direct* or *neighbor-modulated* fitness, which accounts for social behavior from the viewpoint of the recipients of social acts (Frank, 1998; Hamilton, 1970). Alternatively, we can think that an altruistic individual may increase the transmission of the genes for altruism that reside in its recipients' bodies, as long as there are positive associations between the actor and its recipients. Thus the fitness of an individual is affected not only by its own phenotype but also by its effect on its neighbor's fitness. This is called *inclusive* fitness, which accounts for social behavior from the viewpoint of the actor itself (Hamilton, 1964).

The two ways of analyzing interactions between individuals reach a mathematically equivalent conclusion, i.e., *Hamilton's rule*. The rule states that a social trait will be favored by selection if $rB > C$, where B is the fitness benefit to the recipient, C is the fitness cost to the actor, and r is the regression coefficient of relatedness between individuals. Since common genealogy is the most common source for generating statistical associations between individuals, Hamilton's theory of social evolution is often called *kin selection* theory (Maynard Smith, 1982). Yet it is worth noting that the regression coefficient of relatedness is more general than genealogical relatedness (Frank, 1998; Hamilton, 1964, 1970). Hamilton's rule specifies the condition for the increase of a gene for helping genetic relatives at a cost to the actor itself; thus it represents a unified theory for family relationships (Mock & Parker, 1997).

Conflicts within the family

Trivers (1974) contended that families are not necessarily harmonious and peaceful enclaves, which would exhibit internal conflict only when they become somehow "dysfunctional." Rather, the family should be regarded as a social unit rife with evolutionary conflicts of interests between all family members over the flow of parental investment (PI) from parent(s) to offspring. Although family members have partly overlapping interests, they are not genetically identical and hence conflicts of interests are predicted to ensue.

There could be three major forms of evolutionary conflict within the family (Mock & Parker, 1997; see Figure 1.2). First, *parental conflict* may occur concerning how much PI each parent should give to their offspring within the family. Either parent will benefit if its partner provides more PI. Second, *parent-offspring conflict* may occur concerning how much PI the parent(s) should provide to their offspring. Offspring are designed to 'want' more PI than the parent is designed to give. Third, *sibling conflict* may occur concerning the amount of PI that each sibling should obtain. Siblings within

a family compete with each other to gain more resources. The actual level of PI as observed in nature should be the simultaneous resolution of all three evolutionary games between family members.

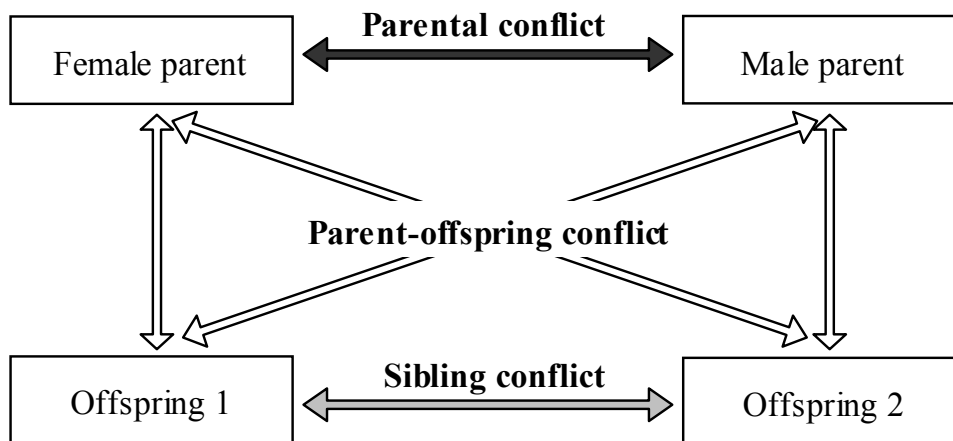


Figure 1.2. Three major forms of conflicts within families.

Parent-offspring conflict

Trivers' (1974) theory of parent-offspring conflict applies Hamilton's rule to analyze parent-offspring interactions. An offspring is related to itself ($r = 1.0$) two times greater than its siblings ($r = 0.5$ if full siblings); hence it will value itself higher than its sibling. A female parent, however, is equally related to all of her offspring ($r = 0.5$) (the same is true for a male parent if he fertilized all offspring). All else being equal, i.e., if there were no differences in each offspring's states like age, sex, or physiological condition, a mother is expected to equally invest into all offspring. Therefore, selection acts on genes expressed in parents and young in different ways such that an offspring insists more resources than the parent is willing to give.

A concrete example may help understand the potential genetic conflict between parent and offspring (see Figure 1.3). Consider a parent looking after her single

offspring. Offspring fitness is assumed to be an increasing function $f(x)$ of the amount of PI, x , that it receives from the parent, with diminishing returns. The parent suffers a linear cost in terms of her future reproductive success, which is given by $g(x) = G + bx$ (G is a positive constant and $b (< 0)$ measures the marginal cost of parental care). The parent's inclusive fitness is now written as $W_p = f(x) + g(x)$. Maximizing W_p with regard to x gives the parent's evolutionarily stable (ESS) amount of PI:

$$\left[\frac{\partial}{\partial x} W_p = f'(x) + g'(x) = f'(x) + b \right]_{x=x_p^*} = 0, \quad (1.1)$$

where the prime denotes differentiation with respect to x . The ESS amount of PI from the parent's point of view lies in the point x_p^* at which the marginal benefit from additional resources ($f'(x)$) is equal to the marginal cost of investing into the current offspring, with opposite sign ($-b$). Graphically, it is when a line with a positive slope ($-b$) is tangent to the offspring fitness curve $f(x)$. By contrast, the offspring's inclusive fitness is written as $W_o = f(x) + \frac{1}{2}g(x)$, where we assume full siblings for convenience. Maximizing W_o gives the offspring's evolutionarily stable (ESS) amount of PI:

$$\left[\frac{\partial}{\partial x} W_o = f'(x) + \frac{1}{2}g'(x) = f'(x) + \frac{1}{2}b \right]_{x=x_o^*} = 0. \quad (1.2)$$

The ESS amount of PI from the offspring's point of view lies in the point x_o^* at which a line with a less steep slope ($-\frac{1}{2}b$) is tangent to the offspring fitness curve $f(x)$. Figure 1.3 shows that the optimal PI from the offspring's point of view, x_o^* , is necessarily greater than the optimal PI from the parent's point of view, x_p^* . Up to x_p^* , both participants agree to increase PI. However, between x_p^* and x_o^* there exists a range of PI over which the best parental strategy is to decrease PI, but the best offspring strategy is to increase PI. The zone of parent-offspring conflict indicates the presence of potential genetic 'battleground' over the amount of PI between parent and offspring. Beyond x_o^* , both participants agree to decrease PI (Godfray, 1995, 1999; Mock & Parker, 1997).

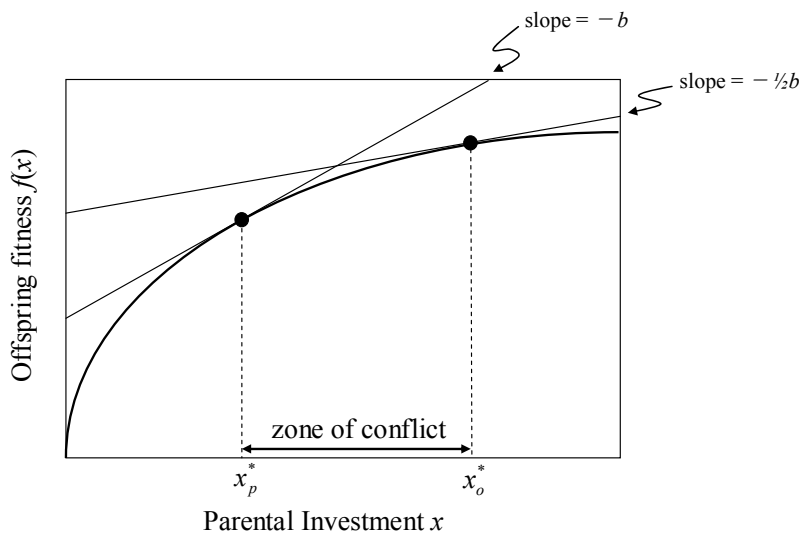


Figure 1.3. A graphical illustration of the battleground of parent-offspring conflict.

Scramble competition models vs. honest signaling models

Theoretical models of family relationships have often employed vigorous begging displays of nestling birds as a model system to predict the ESS allocation of parental resources among offspring (Mock & Parker, 1997; Wright & Leonard, 2002). Begging was initially interpreted as the outcome of scramble competition among nestlings under offspring's control over resource allocation (Macnair & Parker, 1979; Parker & Macnair, 1979). Recent models of honest-signaling suggest that begging displays honestly advertise offspring's cryptic condition (e.g., hungry level) to parents who control resource allocation (Godfray, 1991, 1995a).

REPRODUCTIVE VALUE AND THE HUMAN FAMILY

Despite a number of mathematically sophisticated models of intrafamilial conflict, behavioral ecologists often complain that current theoretical models are too unrealistic to forcefully guide their empirical research in the laboratory and the field

(Mock & Parker, 1997; D. Mock, 2005, personal communication). No wonder evolutionary psychologists concerned with human families acknowledge that “the available models offer psychologists *only broad guidelines* [italics added] about cooperative and competitive behavior among kin” (Kurland & Gaulin, 2005, p. 456).

One serious limitation of current evolutionary models of intrafamilial interactions is that all individuals in the population are assumed to be of the same class. That is, it is assumed that individuals following a certain strategy are all identical in their probability of survival and reproductive output. The assumption makes it possible to characterize the fitness of a strategy simply as the total number of offspring produced over the lifetime of an individual following the strategy. However, in many (perhaps most) cases, individuals can be more than one class. They may differ, for example, in age, sex, size, developmental stage, or physiological condition (e.g., fat stores), which is fairly obvious to both field behavioral ecologists and human psychologists. Since offspring following a given strategy may differ in their state and hence in their ability to produce offspring in the next generation, we can no longer evaluate the fitness of a strategy simply by counting offspring (Charlesworth, 1994; Houston & McNamara, 1999; Taylor, 1990). Then, how could we evaluate the fitness of PI allocation strategy among offspring of more than one class?

Fisher’s (1930) concept of reproductive value provides the solution. Reproductive value measures the relative contributions of individuals of different classes to the ancestry of future generations; thus it functions as a weighting factor for the effect of a strategy on offspring belonging to different classes. Recently, a formal method that applies the concept of reproductive value to determine the evolutionarily stable strategy (ESS) in a class-structured population has been established (a strategy is said to be ESS if it is adopted by all members of the population then no other strategy could replace it) (Frank, 1998; Pen & Weissing, 2002; Taylor, 1990; Taylor & Frank, 1996a). The reproductive value approach weights the costs and benefits of both the actor (parents)

and the recipients (offspring) with class-specific reproductive value, thus finding out a proper fitness measure for a certain PI allocation strategy. The proper fitness measure is often called ‘invasion fitness’, one that is given by the asymptotic population growth rate of a mutant subpopulation relative to the growth rate of the resident population (Metz, Nisbet, & Geritz, 1992). If a population is ESS with respect to parents’ resource allocation strategy among different-aged offspring, any invading mutant strategy should have a lower rate of asymptotic growth than the resident strategy. The asymptotic growth rate of the mutant must thus be at a local maximum when it adopts the optimal allocation strategy.

In this dissertation, I explicitly make use of reproductive value approach to construct an evolutionary model of family interactions. Given that age difference commonly results in divergent reproductive value among individuals, such an evolutionary model is applicable to a wide variety of organisms that are structured into distinct age classes. The approach is especially valuable for analyzing human family systems, where children within a household are of different ages and have a very long developmental period, relative to other comparably sized primates (Bogin, 1997; Geary & Flinn, 2001).

In humans, the period of offspring dependency extends well past the typical age of weaning (usually between ages 3 and 4 years in traditional societies) into the childhood period. Throughout the period of offspring dependency, offspring survival critically depends on parental caregiving (Bjorklund & Pellegrini, 2002). Humans’ prolonged immaturity is hence considered “a hallmark of our species and is responsible, in large part, for many of our cognitive and behavioral features” (Bjorklund & Younger, 2001, p. 64). Consequently, constructing an ESS model for the family systems that are structured into age classes will provide valuable insights into the adaptive design features of human psychological mechanisms governing parental and child psychology over the distribution of parental resources within the family.

CHAPTER OVERVIEW

In chapter 2, I show how a class-structured ESS model based on age-specific reproductive value could be constructed for analyzing the flow of parental resources from parent(s) to offspring of different age classes. In chapter 3, I attempt to test *a priori* predictions about human parental favoritism among different-aged children by asking human participants. In chapter 4, I theoretically investigate the genetic ‘battleground’ in which the evolutionary interests of each family member (a parent, older offspring, and younger offspring) collide with each other in a subtle but crucial way. In chapter 5, I study the differential altruistic tendency toward cousins, demonstrating that Hamilton’s insight is also valuable for elucidating our evolved psychology toward distant kin. In the final chapter, I review the major results of the dissertation and suggest directions for future research.

Chapter 2: Parental Favoritism among Different-aged Offspring

SUMMARY

The theories of intrafamilial conflict and parental investment have yet to examine how parental decision to allocate its resources is influenced by the fact that its offspring may not be identical, but classified into distinct age classes. Two counteracting effects of offspring growth on parental allocation of resources have deterred the development of a formal model: a parent may favor its older offspring due to their greater reproductive value and yet favor its younger offspring due to their higher marginal returns from extra resources. Using evolutionary invasion analysis in class-structured populations, I present a formal model that explores how a parent should allocate its resources among different-aged offspring from the viewpoint of parents. The parent's evolutionarily stable strategy is to allocate its resources such that the marginal benefit to each offspring's survival, devalued by the survival probability to the reproductive age, is equal to the marginal cost to the parent's residual survival. Two general situations are considered in which younger offspring obtain higher marginal returns than older offspring. In nearly all circumstances, parents are expected to bias its resources toward older offspring. The result may well account for a widespread yet puzzling phenomenon in view of previous theories of intrafamilial conflict.

INTRODUCTION

Parents are expected to adaptively allocate their limited resources among offspring so as to maximize parental fitness (Clutton-Brock, 1991; Smith & Fretwell, 1974; Winker, 1987). Yet offspring may be selected to demand more resources than parents are selected to provide (Trivers, 1974), which leads to various conflicts between family members over the flow of parental investment. Vigorous begging displays of

nestling birds are often employed as a model system to predict the evolutionarily stable (ES) level of parental investment among offspring (Mock & Parker, 1997). Begging was initially interpreted as the outcome of scramble competition among nestlings under offspring's control over resource allocation (Macnair & Parker, 1979; Parker & Macnair, 1979). The alternative model suggests that begging displays honestly advertise offspring's cryptic condition (defined as offspring's marginal fitness gain from obtaining extra resources) to parents who control resource allocation within broods (Godfray, 1991, 1995b). The honest-signaling model predicts that parents should invest more in needier offspring, which are supported by a number of empirical evidence that hungrier nestlings indeed beg more and receive more food from their parents (Kilner & Johnstone, 1997).

Within-brood resource allocation, however, must be shaped not only by offspring's cryptic internal condition (commonly called as 'need') but by offspring's external condition that parents may directly access, such as offspring's age, sex, and competitive ability (Glassey & Forbes, 2002). In particular, age differences among offspring are very common in asynchronously hatching birds and many mammals. Hatching asynchrony in altricial birds greatly influences food allocation among nestlings with earlier-hatched (older) nestlings getting more food, leading to the higher mortality of later-hatched (younger) nestlings (Magrath, 1990). These findings have been interpreted as the consequence of scramble competition among nestlings where parents exert little or no control over resource distribution (Macnair & Parker, 1979; Parker & Macnair, 1979). Yet, parents may have full or much control over food distribution and preferentially invest into older offspring. Even when parents seem to passively feed more competitive offspring, it may be in parental interests to do so. Therefore, to understand how both cryptic and noncryptic conditions of offspring affect intrafamily social dynamics, it is necessary to elucidate the optimal distribution of resources among different-aged offspring from the viewpoint of parents.

Unfortunately, no formal treatments have been made about how parents should allocate resources among their different-aged offspring (Clutton-Brock, 1991). Making realistic predictions about the issue has been considered very difficult, due to the mutually counteracting effects of offspring growth on the ES level of parental provisioning. On one hand, parents may favor older offspring because older offspring have higher reproductive value, i.e., greater genetic contribution far into the future generation (Fisher, 1930). This is both because older offspring are closer to reproductive maturity and because the instantaneous rate of juvenile mortality tends to decrease with increasing age. On the other hand, parents may favor younger offspring because younger offspring have higher needs for food than older offspring: the effect of additional investment on offspring survival will be higher for younger offspring (Clutton-Brock, 1991; Rubenstein, 1982; Sargent & Gross, 1986).

Recent empirical studies of food allocation in asynchronously hatched broods pose a serious problem for extant models of parent-offspring interactions (Cotton, Wright, & Kacelnik, 1999; Lotem, 1998; Smiseth, Bu, Erikenaes, & Amundsen, 2003). According to the honest-signaling model's definition of need, younger (smaller) nestlings are in greater need for food; hence they are expected to beg more vigorously and to be fed more often than older (larger) nestlings. Surprisingly, many experimental studies have found that older nestlings actually receive more food, even though they beg less intensively than their younger siblings (Kilner, 1995; Lotem, 1998; Price, Harvey, & Ydenberg, 1996; Smiseth et al., 2003). This striking discrepancy between theoretical predictions and empirical findings may indicate that fundamental aspects of parent-offspring interaction have yet to be understood (Cotton et al., 1999). Meanwhile, the scramble competition model predicts that the older offspring with high competitive ability would get more food than the younger offspring, which coincides with most observed allocation patterns in asynchronously hatched broods (Mock & Parker, 1997; Parker, Royle, & Hartley, 2002a). However, age discrepancy cannot be simply equated

to competitive asymmetries among offspring. Offspring of the same age may still show considerably different competitive abilities because they may differ in, say, general health. Also, the age differences among offspring bring about a number of physiological and developmental changes, not all of which are translated into competitive asymmetries (Glassey & Forbes, 2002). It is thus unclear if the observed biased distribution of foods toward older offspring could be solely attributable to the competitive asymmetries per se. Moreover, as shown above, there remains the unresolved possibility that parents may have much or full control over food distribution and actively prefer feeding their older offspring. Indeed, recent empirical evidence indicates that parents may play an active role in food allocation within asynchronous broods (Kilner, 1995; Krebs, Cunningham, & Donnelly, 1999; Smiseth et al., 2003).

To accurately assess the consequences of parental allocation of resources among offspring of different ages, it is necessary to construct evolutionary models of class-structured populations in which individuals fall into different age classes. In such models, Fisher's (1930) concept of reproductive value acts as a weighting factor for comparing the effects of changes in age-specific survival or fecundity on a common scale (Charlesworth, 1994; Frank, 1998; Pen & Weissing, 2002; Taylor, 1990; Taylor & Frank, 1996b). Here, I present a model that investigates how a parent should invest into its offspring who are classified into different age classes. Within the model's life-history framework based on reproductive value, the effect of additional food on younger offspring's survival will be allowed to be higher than older offspring's survival. The model presented here thus integrates the two counteracting effects of offspring growth on parents' allocation strategy within broods.

THE MODEL

Dynamics of resident population

Consider a diploid resident population that is structured into parents (class P) and their offspring classified into n age classes (class O_i : $i = 1, \dots, n$). For simplicity, I assume hermaphroditic individuals that reproduce as both male and female. After mating with another adult, a single parent produces $2f$ offspring per time step and allocates its limited resources among all offspring of differing ages. Since one-half of the $2f$ newborn offspring are credited to its mate, the parent actually expects fitness credit for f offspring. The population is further structured into distinct broods, in which each parent provisions only their own offspring within the brood. The length of the time step in this system corresponds to the average age gap between siblings; it will be measured in days for asynchronously hatching birds whereas it will typically be measured at a larger time scale for mammals (The model thus focuses on within-year dynamics for the case of asynchronously hatching birds). Given that offspring provisioning usually occurs over a considerable period of time, it would be desirable to consider the dynamic (i.e., time-dependent) aspects of parent-offspring interactions as well. Unfortunately, such an analysis is extremely difficult to be carried out. Following other authors (e.g., Godfray, 1995a, 1995b; Johnstone, 2004; Parker, Mock, & Lamey, 1989; Rodriguez-Girones, Cotton, & Kacelnik, 1996), I assume that, for each time step, the parent-offspring interaction is composed of a series of feeding events and that the outcome of each event has an independent effect on the fitness of allocation strategy.

At each feeding event during a time step, a focal parent invests in its current brood composed of different-aged offspring, at a cost of the parent's future survival. The average number of age- i offspring per adult in the population is denoted as u_i . The per capita amount of resources that an age- i offspring receives is x_i . Thus the total amount of resources an average parent provisions for its current brood per each time

step is proportional to $E_x = \sum_{i=1}^n u_i x_i$. An average parent's allocation strategy is denoted by a vector $\mathbf{x} = [x_1, x_2, \dots, x_n]$, where each trait value x_i can be estimated by its genotypic value plus the unexplained residual. It is assumed that the n trait values are genetically uncorrelated with each other. An age- i offspring survives and grows into an offspring aged $i + 1$ to the next time step with survival probability $\varphi_i = \varphi_i(x_i)$, which is assumed to be an increasing function of x_i . A focal parent survives to the next time step with probability $\psi = \psi(E_x)$, a decreasing function of E_x . Figure 2.1 depicts the life cycle for the resident population. The population transition matrix \mathbf{A} corresponding to fig. 2.1 is

$$\mathbf{A} = \begin{bmatrix} 0 & 0 & \dots & 0 & f \\ \varphi_1(x_1) & 0 & \dots & 0 & 0 \\ 0 & \varphi_2(x_2) & \dots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \dots & \varphi_n(x_n) & \psi(E_x) \end{bmatrix}. \quad (2.1)$$

The resident population characterized by the matrix \mathbf{A} will eventually reach a constant rate of geometric growth: $\mathbf{A}^* \mathbf{u}^* = \lambda \mathbf{u}^*$, where λ is the dominant eigenvalue of the resident matrix \mathbf{A}^* at equilibrium and the column vector of stable age distribution $\mathbf{u}^* = [u_1^*, u_2^*, \dots, u_n^*, u_p^*]$ is the dominant right eigenvector of \mathbf{A}^* . Since \mathbf{u}^* is determined up to a constant, I let the number of parental class u_p^* equal 1.0 so that u_i^* could represent the average number of age- i offspring per adult in the population at equilibrium. The row vector of individual reproductive values $\mathbf{v}^* = [v_1^*, v_2^*, \dots, v_n^*, v_p^*]$ is the dominant left eigenvector of \mathbf{A}^* : $\mathbf{v}^* \mathbf{A}^* = \lambda \mathbf{v}^*$. The two vectors \mathbf{u}^* and \mathbf{v}^* are obtained in Supplemental data 2.1.

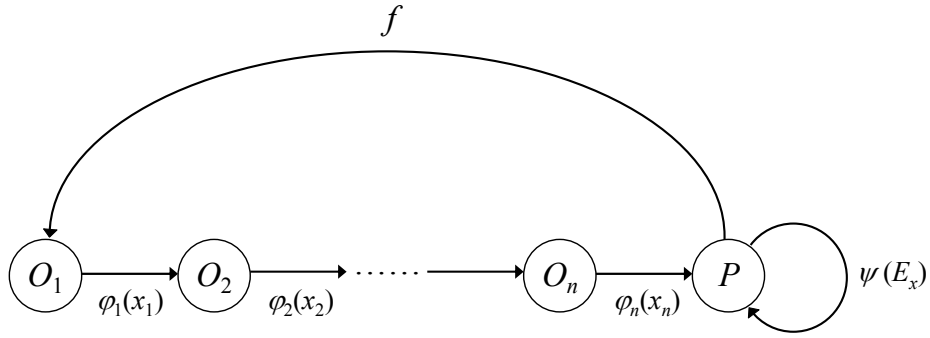


Figure 2.1. A life cycle graph for an age-classified population with a parental class and n different-aged offspring classes. The arcs indicate transitions between age classes; the symbols labeling each arc indicate the contribution of each age class to another.

It is unrealistic, however, to expect that the resident population will grow indefinitely: density-dependent factors will ensure that the population size is no longer changing. The constraint $\lambda = 1$ requires the following equation to be satisfied:

$$f\varphi_1(x_1^*)\varphi_2(x_2^*)\dots\varphi_n(x_n^*) = 1 - \psi(E_x^*), \quad (2.2)$$

where $E_x^* = \sum_{i=1}^n u_i^* x_i^*$. Equation 2.2 means that, by the operation of density dependence, the rate at which new reproducing adults are introduced into the population (the left-hand side) is balanced by the death rate of existing adults (the right-hand side). The assumption of density dependence implies that we need to decide which vital rate(s) in the life cycle will be influenced by the population density (Mylius & Diekmann, 1995; Pen & Weissing, 2000, 2002). Since density-dependent factors tend to act on offspring survival, particularly for bird populations (Charnov, 1993; Ricklefs, 2000), I assume that the age-1 offspring survival ($\varphi_1(x_1)$) can be expressed in terms of other vital rates such that equation 2.2 is satisfied (in this system, it does not make any difference if we choose other vital rates to be density dependent).

Given that it takes n time steps for a newborn offspring to become an adult, one

may ask the fate of a parent's brood in case the parent dies during the n time steps. Perhaps the whole brood will instantly die due to the lack of parental provisioning, which will change the transition matrix in equation 2.1. This difficulty to intuitively understand the model situation is common in evolutionary models of class-structured populations, and can be overcome by following Taylor's (1990; 1996) suggestion: "an individual who survives to the next generation with probability p is regarded as dying and contributing p "offspring" to the appropriate class" (Taylor, 1996, p. 663). Thus, an average parent in the current model can be regarded as producing ψ "offspring" to the parental class as well as f real offspring to the age-1 class. Each age- i offspring produces φ_i "offspring" to the age $i+1$ class. Since individuals of different age classes differ in terms of the age mix of their "offspring", we can correctly weight their fitness contributions by the corresponding reproductive value, as shown below.

Invasion analysis

To find the ES allocation strategy among different-aged offspring, we seek under what conditions a rare mutant allocation strategy $\mathbf{x}^\circ (= [x_1^\circ, \dots, x_n^\circ])$, where $x_i^\circ = x_i + \Delta x$ can invade the resident population fixed for the resident strategy \mathbf{x}^* . The mutant strategy \mathbf{x}° is assumed to be rare enough that the average number of age- i offspring per mutant adult is given by u_i^* , i.e., the offspring age distribution in the resident population with \mathbf{x}^* . The transition matrix of the mutant subpopulation is:

$$\mathbf{A}(\mathbf{x}^\circ, \mathbf{x}^*) = \begin{bmatrix} 0 & 0 & \dots & 0 & f \\ \varphi_1(x_1^\circ) & 0 & \dots & 0 & 0 \\ 0 & \varphi_2(x_2^\circ) & \dots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \dots & \varphi_n(x_n^\circ) & \psi(E_x^\circ) \end{bmatrix}, \quad (2.3)$$

where $E_x^\circ = \sum_{i=1}^n u_i^* x_i^\circ = \sum_{i=1}^n f \varphi_1^* \varphi_2^* \dots \varphi_{i-1}^* x_i^\circ$ (see Supplemental data 2.1).

The invasion fitness of a mutant strategy \mathbf{x}° is sought as the initial growth rate of mutant subpopulation in the resident population, i.e., the dominant eigenvalue $\lambda(\mathbf{x}^\circ, \mathbf{x}^*)$ of $\mathbf{A}(\mathbf{x}^\circ, \mathbf{x}^*)$ (Metz *et al.*, 1992). Therefore, for a resident strategy \mathbf{x}° to be evolutionarily stable, $\lambda(\mathbf{x}^\circ, \mathbf{x}^*)$ should have a local maximum at $\mathbf{x}^\circ = \mathbf{x}^*$ such that:

$$\left. \frac{\partial \lambda(\mathbf{x}^\circ, \mathbf{x}^*)}{\partial \mathbf{x}^\circ} \right|_{\mathbf{x}^\circ = \mathbf{x}^*} = 0, \quad (2.4)$$

and the Hessian matrix of $\lambda(\mathbf{x}^\circ, \mathbf{x}^*)$ is negative semi-definite (i.e., all of its eigenvalues is less than or equal to zero) at the equilibrium point (x_1^*, \dots, x_n^*) (Leimar, 2001; Day & Taylor, 2003). The first-order condition for a strategy \mathbf{x}^* to be an ESS can be rewritten as the following n equations:

$$\mathbf{v}^* \left. \frac{\partial \mathbf{A}(\mathbf{x}^\circ, \mathbf{x}^*)}{\partial x_i^\circ} \right|_{x_i^\circ = x_i^*} \mathbf{u}^* = 0 \quad (i = 1, \dots, n). \quad (2.5)$$

Note that, although the correct fitness measure of a rare mutant strategy \mathbf{x}° is $\lambda(\mathbf{x}^\circ, \mathbf{x}^*)$, we can instead use $W(\mathbf{x}^\circ, \mathbf{x}^*) = \mathbf{v}^* \mathbf{A}(\mathbf{x}^\circ, \mathbf{x}^*) \mathbf{u}^*$ as the fitness function because $\partial \lambda / \partial \mathbf{x}^\circ$ and $\partial W / \partial \mathbf{x}^\circ$ have the same sign (Taylor & Frank, 1996). From equation 2.5 and Supplemental data 2.1, a parent's ES allocation strategy \mathbf{x}^* ($= [x_1^*, \dots, x_n^*]$) is obtained by n equilibrium conditions as follows:

$$\begin{aligned} (\varphi_2^* \varphi_3^* \dots \varphi_n^*) \varphi_1'(x_1^*) &= -\psi'(E_x^*) \\ (\varphi_3^* \dots \varphi_n^*) \varphi_2'(x_2^*) &= -\psi'(E_x^*) \\ &\vdots \\ \varphi_n'(x_n^*) &= -\psi'(E_x^*) \end{aligned} \quad (2.6)$$

where the prime denotes differentiation of a function with respect to its argument and $E_x^* = \sum_{i=1}^n u_i^* x_i^*$. The n equilibrium conditions emphasize that the n trait values comprising the vector of allocation strategy are coevolving. Equation 2.6 indicates that, at the ES allocation from a parent's viewpoint, the marginal benefit of additional resources to each offspring's survival $\varphi_i'(x_i^*)$, weighted by the survival probability of each offspring to the reproducing age (i.e., $\varphi_{i+1}^* \varphi_{i+2}^* \dots \varphi_n^*$), is equal to the marginal cost of current total

expenditure to the parent's residual survival $\psi'(E_x^*)$. The second-order condition for evolutionary stability, as well as the condition for convergence stability, is checked in Supplemental data 2.2.

RESULTS

To derive concrete predictions on the parental ES allocation of resources among different-aged offspring, I allow the effect of additional resources on younger offspring's survival to be greater than on older offspring's survival, in accordance with previous research (Clutton-Brock, 1991; Rubenstein, 1982; Sargent & Gross, 1986; West-Eberhard, 1975). There are two general situations where a younger offspring would have higher needs for food than an older offspring. First, the marginal benefit of additional resources may be always higher for a younger offspring than an older offspring, no matter how much resources were already provided during a given feeding episode. Alternatively, the marginal benefit of resources may be higher for a younger offspring only when the resources already provided are none or few (i.e., when both offspring are equally hungry); if the resources provided are relatively high (i.e., when both offspring were equally fed well), the marginal gain of additional resources would be higher for the older offspring. Indeed, once enough resources have been equally distributed between the older and younger offspring, the latter's survival will hardly increase with additional resources whereas the former's survival will still have room to increase. The second situation appears more plausible and is what previous researchers have had in mind (Clutton-Brock, 1991; Rubenstein, 1982; Sargent & Gross, 1986). In both situations, I assume that a parent completely controls both the total amount of resources delivered and the division of the resources to each individual offspring.

The ES pattern of parental resource allocation can be obtained as follows. The survival probability of an offspring is assumed to increase with the resources provided,

with diminishing returns (i.e., $\varphi'(x) > 0$, $\varphi''(x) < 0$) (e.g., Smith & Fretwell, 1974). Consider two offspring spaced by one time step. At evolutionary equilibrium, each offspring will receive its ES level of resources (i.e., x_i^* and x_{i+1}^* , where $i = 1, \dots, n-1$) from the parent. Since $\varphi'(x)$ is a decreasing function of x , whether x_i^* is larger or smaller than x_{i+1}^* can be determined by comparing the younger offspring's marginal return at x_i^* with its marginal return at x_{i+1}^* (i.e., comparing $\varphi'_i(x_i^*)$ with $\varphi'_i(x_{i+1}^*)$, respectively). Let us denote $\varphi'_i(x_i^*) - \varphi'_i(x_{i+1}^*)$ by δ . Reflecting the equilibrium conditions in equation 2.6, δ can be rewritten as:

$$\delta = \varphi'_i(x_i^*) - \varphi'_i(x_{i+1}^*) = \frac{\varphi'_{i+1}(x_{i+1}^*)}{\varphi_{i+1}(x_{i+1}^*)} - \varphi'_i(x_{i+1}^*), \quad (2.8)$$

the sign of which informs whether x_i^* is larger or smaller than x_{i+1}^* . For instance, the plus sign of δ indicates that x_i^* is less than x_{i+1}^* (i.e., the older offspring receives more resources than the younger offspring at ESS).

A younger offspring yields higher marginal returns for every level of resources provided

If a younger offspring could obtain a higher marginal return than an older offspring for every level of resources provided by the parent during a given feeding episode (i.e., $\varphi'_i(x) > \varphi'_{i+1}(x)$ for all x), then it can be shown that $\delta = \varphi'_i(x_i^*) - \varphi'_i(x_{i+1}^*) > 0$ for all levels of x (see Supplemental data 2.3 for the proof). Since $\varphi'(x)$ decreases with x , it is revealed that $x_i^* < x_{i+1}^*$. Therefore, rather surprisingly, if a younger offspring yields higher marginal returns than an older offspring for every level of resources provided during a feeding bout, then the parent's ES allocation strategy \mathbf{x}^* ($= [x_1^*, \dots, x_n^*]$) is to distribute its resources such that older offspring get more resources than younger offspring (i.e., $x_1^* < x_2^* < \dots < x_n^*$).

I illustrate the above result by assuming explicit functions for an age- i offspring survival:

$$\varphi_i(x_i) = K_i[1 - \exp(-cx_i)], \quad (2.9)$$

where K_i is a positive constant denoting the asymptotic level of offspring survival ($0 < K_i \leq 1$) and c , so-called ‘shape constant’ (Parker et al., 1989), defines the rate at which $\varphi_i(x_i)$ rises to K_i . Offspring of distinct ages differ only in their asymptotes: K_i is assumed to be larger than K_{i+1} , which ensures $\varphi'_i(x_i^*) > \varphi'_{i+1}(x_{i+1}^*)$ for every value of x (Fig. 2.2a). In other words, the asymptote K_i of an age- i offspring survival curve will be inversely related to the offspring’s age: $K_1 > K_2 > \dots > K_n$. Throughout this chapter, I assume that the parent’s residual survival is an exponentially decreasing function of current parental expenditure (i.e., each increment of parental investment is more costly than the previous increment):

$$\psi(E_x) = G - a \cdot \exp(bE_x) = G - a \cdot \exp\left(b \sum_{i=1}^n u_i^* x_i\right), \quad (2.10)$$

where a and b are positive parameters that specify how the total amount of resources provided to the current brood reduces the parent’s residual survival and G is a positive constant. The ES allocation of resources in asynchronous broods with two offspring is given in Fig. 2b. Despite (in fact, because of) the younger offspring’s higher marginal return for any level of resources provided, the parent will invest more resources into the older offspring than the younger offspring. It can also be seen that the larger the difference between the asymptotes of each offspring (i.e., the larger the age spacing between the two offspring), the more favored the older offspring.

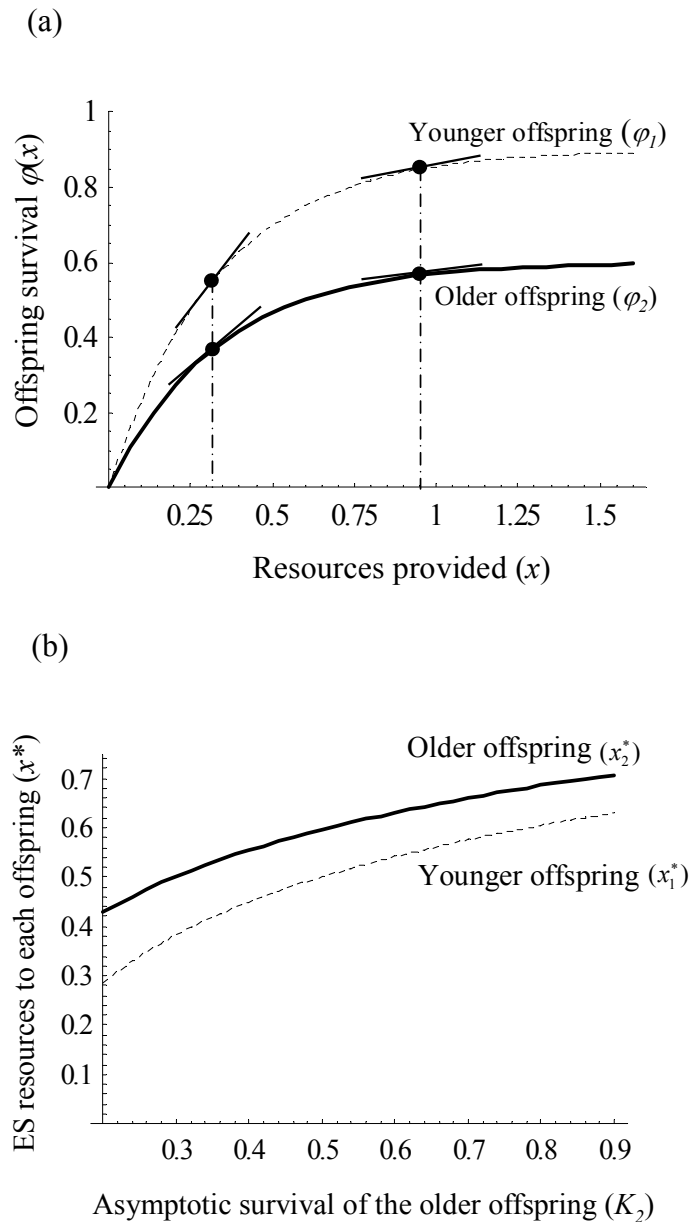


Figure 2.2. A situation in which a younger offspring yields higher marginal returns than an older offspring, for every level of resources provided. (a) The survival probabilities of each offspring ($\varphi(x)$) as a function of the resources provided (x) during a single feeding episode. The slope of the tangent line to a survival curve at the point $(x, \varphi(x))$, that is, $\partial\varphi(x)/\partial x$, is higher for the younger offspring's curve φ_1 than the older offspring's curve φ_2 , no matter what value of x may be. Parameters are $K_1 = 0.9$, $K_2 = 0.9$, and $c = 3$. (b)

The ES amounts of resources (x^*) that the parent will deliver to each offspring, when the older offspring's asymptote K_2 is varied with the younger offspring's asymptote K_1 being fixed at 0.9. The equilibrium values were obtained from eqn 6 for two different-aged offspring: $\varphi_2(x_2^*)\varphi_1'(x_1^*) = \varphi_2'(x_2^*) = -\psi'(fx_1^* + f\varphi_1(x_1^*)x_2^*)$. Other parameters are $c=3$, $f=1$, $a=0.1$, and $b=1$.

A younger offspring yields higher marginal returns only when the resources already provided are none or few.

Suppose that a younger offspring yields a higher marginal return than an older offspring with none or few resources provided, but it yields a lower marginal return with high resources. In this situation, it can be proved that $\delta = \varphi_i'(x_i^*) - \varphi_i'(x_{i+1}^*)$ is positive and hence $x_i^* < x_{i+1}^*$ (see Supplemental data 2.4 for the proof). Therefore, as in the previous situation, the parent's ES allocation is to bias its resources in favor of older offspring (i.e., $x_1^* < x_2^* < \dots < x_n^*$).

To illustrate the above result, let an age- i offspring's survival be given by

$$\varphi_i(x_i) = K[1 - \exp(-c_i x_i)], \quad (2.11)$$

where the shape constant c_i is allowed to vary according to offspring's distinct age. To ensure that $\varphi_i'(x_i^*) > \varphi_i'(x_{i+1}^*)$ for small values of x and yet $\varphi_i'(x_i^*) < \varphi_i'(x_{i+1}^*)$ for large values of x , c_i is assumed to be larger than c_{i+1} . In other words, the shape constant c_i of an age- i offspring survival curve will be inversely related to the offspring's age: $c_1 > c_2 > \dots > c_n$ (Fig. 2.3a) (Sargent & Clutton-Brock, 1991; Sargent & Gross, 1986). This is consistent with the honest-signaling models' assumption that the survival curve of 'needier' (hence younger) offspring is regarded as having a greater c value; yet the

honest-signaling models (incorrectly) contend that the younger offspring yields a higher marginal return no matter what value of x is provided (Godfray, 1991, 1995a).

Figure 2.3b gives the ES allocation of resources among two different-aged offspring with the younger offspring's shape constant c_1 being fixed at a certain value. As expected, despite the younger offspring's higher marginal return with none or few resources provided, the parent will preferentially invest into the older offspring over the range of the older offspring's shape constant c_2 (i.e., when the age difference between two offspring is varied). The graph also reveals that, as c_2 decreases while c_1 is fixed (hence the older offspring's age increases compared to the younger offspring's fixed age), the older offspring's resource share increases and the younger offspring resource share, to a lesser extent, decreases. In other words, the larger the age spacing between two siblings, the more favored the older offspring.

In terms of the explicit functions examined above, the survival curves of younger and older offspring may differ both in their asymptotic levels of survival (K) and in their shape constants (c). This case is, however, a variation of the second situation in which a younger offspring yields higher marginal returns only when the resources provided are none or few. Hence the main conclusion of biased allocation toward older offspring remains the same (Supplemental data 2.4). On the other hand, it can be argued that two different-aged offspring will differ in their minimum threshold levels of resources for their survival probabilities to start increasing. For instance, the older offspring tend to have a larger body size, thereby requiring a higher threshold level of resources than the younger offspring. I investigated the consequence of different threshold levels of resources between siblings. The analysis revealed that parents will still bias their resources in favor of the older offspring, as long as the older offspring's threshold level of resources is greater than or equal to the younger offspring's threshold. An 'exceptional' allocation favoring the younger offspring may take place if the younger offspring's threshold is sufficiently greater than the older offspring's one; yet it seems

difficult to imagine how a younger offspring's threshold level of resources could be higher than the older offspring's one in natural populations (J. Jeon, unpublished results).

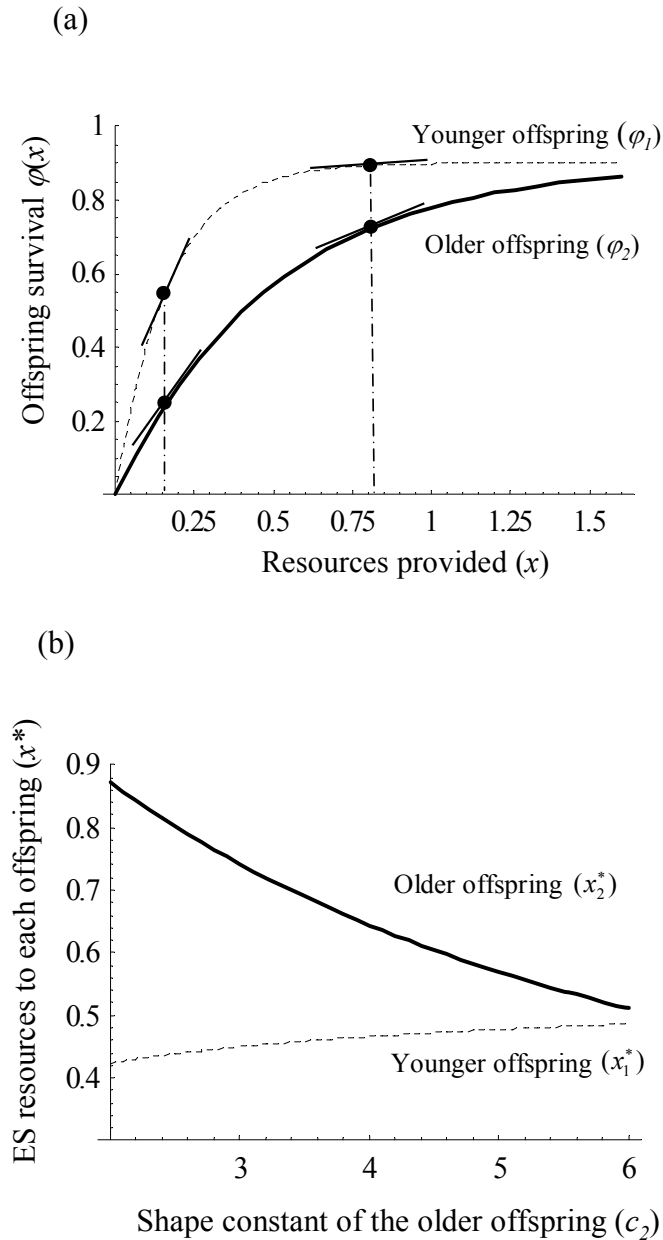


Figure 2.3. A situation in which a younger offspring yields higher marginal returns than an older offspring only when the amount of resources provided is none or few. (a) The survival probabilities of each offspring ($\varphi(x)$) as a function of

the resources provided (x) during a single feeding episode. With a low value of x , the slope of the tangent line to a survival curve at the point $(x, \varphi(x))$, that is, $\partial\varphi(x)/\partial x$, is higher for the younger offspring's curve φ_1 than the older offspring's curve φ_2 ; when x is relatively high, the slope of the tangent line is higher for the older offspring's curve φ_2 . Parameters are $K = 0.9$, $c_1 = 6$, and $c_2 = 2$. (b) The ES amounts of resources (x^*) that the parent will deliver to each offspring, when the older offspring's shape constant c_2 is varied with the younger offspring's shape constant c_1 being fixed at 6. The equilibrium values were obtained from equation 2.6 for two different-aged offspring: $\varphi_2(x_2^*)\varphi_1'(x_1^*) = \varphi_2'(x_2^*) = -\psi'(fx_1^* + fx_2^*\varphi_1(x_1^*))$. Other parameters are $K = 0.9$, $f = 1$, $a = 0.1$, and $b = 1$.

DISCUSSION

Using an evolutionary invasion analysis in class-structured populations, the current model analyzed how a parent should distribute its limited resources among offspring of different ages. At the parent's ESS, the marginal benefit to each offspring's survival, weighted by the survival probability to the reproductive age, is equal to the marginal cost to the parent's residual survival. Following previous discussions, I considered two general situations in which younger offspring obtain a higher marginal return from additional resources than older offspring. It was predicted that a parent would bias its resources in favor of older offspring in nearly all circumstances. The degree of parental favoritism will increase as the age spacing between two offspring increases.

Comparison with traditional allocation theory

Traditional theory for the allocation of limited resources among alternative options suggests that, when offspring vary in quality (e.g., offspring age, sex, or condition), a

parent's optimal allocation is to adjust its investment such that the marginal returns in each offspring are all equal (Haig, 1990; Lloyd, 1985, 1988; Temme, 1986). Accordingly, when offspring are of different ages, a parent's optimal allocation of resources would be to allocate resources in a way that the marginal gains of each offspring's survival are all identical at evolutionary equilibrium: $\varphi'_1(x_1^*) = \varphi'_2(x_2^*) = \dots = \varphi'_n(x_n^*) = -\psi'(x_1^* + \dots + x_n^*)$, where $\varphi'_i(x_i^*)$ is the marginal gain of offspring survival by investing into an age- i offspring and $\psi'(x_1^* + \dots + x_n^*)$ is the marginal cost of current expenditure to the parent's residual survival.

By contrast, the class-structured model presented here shows that the parental ESS is to equalize the marginal gains of each offspring's survival that are devalued by the survival probability to the reproducing age (equation 2.6). In this scheme, the various consequences of the parental actor's investment on the recipient offspring structured into different classes are measured on a common scale, i.e., to what extent current investment into an age- i offspring eventually contributes to the offspring's growth into a reproducing adult. Interestingly, due to the weighting of the survival probability to the reproducing age, the marginal gain from a younger offspring must be higher than an older offspring at the parental ESS: $\varphi'_1(x_1^*) > \varphi'_2(x_2^*) > \dots > \varphi'_n(x_n^*) = -\psi'(E_x^*)$ (see equation 2.8, which shows that $\varphi'_i(x_i^*) = \varphi'_{i+1}(x_{i+1}^*)/\varphi_{i+1}(x_{i+1}^*) > \varphi'_{i+1}(x_{i+1}^*)$). Contrary to the traditional allocation theory insisting the equilibration of marginal gains across all offspring at ESS, the model presented here sheds new insights into the evolution of parental investment allocation: the marginal gains from each offspring are not necessarily equal at ESS. Rather, when offspring are structured into different age classes, the marginal gains from younger offspring will be greater than those from older offspring at the parental ESS. What are equalized in this case are the marginal gains from each offspring that are devalued by the survival probability to the reproducing age. Although the model presented here does not take into account the role of offspring begging, the fact that younger offspring obtain a higher marginal return than older

offspring (i.e., they are ‘needier’) at evolutionary equilibrium may partly explain why younger offspring tend to beg more vigorously than older offspring in real situations.

Implications for models of intrafamilial conflict

The two counteracting effects of offspring growth on parental resource allocation were thought to be 1) older offspring’s higher reproductive value (hence parents should prefer older offspring) and 2) younger offspring’s higher fitness increment with extra resources (hence parents should prefer younger offspring) (Clutton-Brock, 1991). After constructing a structured-population model based on reproductive value, I allowed younger offspring to gain a higher marginal return with additional resources than older offspring, in two general situations. Consequently, the model presented here disentangles and integrates the two counteracting effects of offspring’s growth on parental allocation of resources.

Under nearly all circumstances, the model provides a clear-cut prediction that a parent will preferentially invest into an older offspring over a younger offspring. An ‘exceptional’ allocation favoring younger offspring is possible only when the younger offspring’s threshold level of resources is sufficiently greater than the older offspring’s one, which may be rare in real populations. Nevertheless, there are a handful of studies reporting equal allocation of resources or biased allocation toward younger offspring in asynchronously hatched broods (e.g., Krebs et al., 1999; Leonard & Horn, 1996; Stamps, Clark, Arrowood, & Kus, 1985). It would be interesting to investigate if the precondition of ‘exceptional’ allocation is fulfilled in such species.

Provided that parents win the parent-offspring conflict and hence can impose the parental optimum, the main prediction of biased allocation toward older offspring may well account for the widespread yet enigmatic phenomenon in most asynchronously hatching birds: younger nestlings indeed receive less food than older nestlings, even

though the former beg more intensively (Cotton et al., 1999; Kilner, 1995; Lotem, 1998; Price et al., 1996; Price & Ydenberg, 1995; Smiseth & Amundsen, 2002). Existing models of parent-offspring interactions, lacking in the formal analysis of class-structured populations, have failed to explain such phenomenon. In particular, the honest-signaling models have predicted that parents should bias their resources toward the needier (i.e., younger) offspring, which runs counter to abundant empirical data. The model presented here thus provides a straightforward solution for the hitherto unresolved problem.

In addition to the lack of formal analysis of class-structured populations, the honest signaling models suffer a conceptual problem in defining offspring's cryptic condition (or 'need') in terms of the shape constant c of offspring survival functions. In such models, 'needier' offspring (hungrier offspring as the short-term need; younger (smaller) offspring as the long-term need) correspond to those yielding a higher marginal gain from additional resources (i.e., $\partial\phi/\partial x$) (Price et al., 1996). Unfortunately, in presenting an explicit example for their analysis, the honest-signaling theorists assumed that needier offspring also correspond to those having a lower value of c in their survival functions compared to their sibling (Godfray, 1991, 1995b). In reality, as the Results section shows, the c value of the survival curves does not reliably reflect the marginal gain from extra resources ($\partial\phi/\partial x$): the survival curve with a higher c value may yield either a higher or lower marginal gain than the curve with a lower c value, depending on the amount of resources already provided x (see Fig. 2.3a) (Parker et al., 2002a; Royle, Hartley, & Parker, 2002). Hence, in the honest-signaling models' terminology, younger offspring should not be regarded as being always 'needier', because they will obtain a higher marginal return only when the resources provided are none or few. Future research should focus on clarifying the ambiguous terms like offspring 'need' and 'condition' found in current literature.

Limitations and conclusions

One caveat of the present study is its simplistic assumption that parents always win the parent-offspring conflict and hence the amount of resources transferred in nature is at the parental optimum. Yet the optimal resource allocation from the perspective of each different-aged offspring will actually differ from one another, and it is possible that offspring may (at least partly) win the conflict. Future research should address how the evolutionary conflict among various family members is resolved within an age-dependent life-history context. Furthermore, the present study should be distinguished from Lack's (1947, 1954) interpretation of hatching asynchrony as a low-cost means of adjusting brood size by imposing within-brood competitive asymmetries. The present study simply asked how parents should allocate their resources within asynchronously hatched broods, but not how adaptive brood reduction is made possible due to hatching asynchrony. Nevertheless, the insight that it is in parental interests for older offspring to get more foods may help explain why parents set up within-brood competitive asymmetries in the first place.

Although the theories of intrafamilial conflict, by their very nature, deal with social interactions between individuals of different classes, they have been slow to explicitly model the evolution of class-structured populations. The class-structured model presented here asked how the parental actor's behavior is modulated by the fact that its recipient offspring are not identical but classified into distinct age classes. The model's central prediction appears to well account for the hitherto puzzling phenomenon in view of extant theories, which suggests that the study of intrafamilial conflict and parental investment would benefit from taking advantage of the invasion analysis tool in class-structured populations.

SUPPLEMENTAL DATA

2.1. Reproductive values and stable age distribution

Assuming that λ remains at 1 due to the density-dependent regulation, the vector of individual reproductive values $\mathbf{v}^* = [v_1^*, \dots, v_n^*, v_p^*]$ in the resident population be determined up to a scalar constant from the recurrence equation $\mathbf{v}^* \mathbf{A}^* = \mathbf{v}^*$. Since the eigenvector \mathbf{v}^* can be scaled at will, I choose the reproductive value of parents v_p^* to equal 1. Then the reproductive value of each offspring class is:

$$v_i^* = \prod_{k=i}^n \phi_k^* \quad (i = 1, \dots, n) \quad (2A.1)$$

Likewise, the vector of stable age distribution $\mathbf{u}^* = [u_1^*, \dots, u_n^*, u_p^*]$ can be determined up to a constant from the recurrence equation $\mathbf{u}^* \mathbf{A}^* = \mathbf{u}^*$. By choosing the relative number of parental class u_p^* to 1, I obtain the relative number of each offspring class:

$$u_i^* = f \prod_{k=1}^{i-1} \phi_k^* \quad (i = 2, \dots, n) \quad (2A.2)$$

and u_j is defined as f .

2.2. Evolutionary stability and convergence stability

Here I show that the Hessian matrix (a matrix of second partial derivatives) of $\lambda(\mathbf{x}^\circ, \mathbf{x}^*)$ is negative semi-definite at the equilibrium point (x_1^*, \dots, x_n^*) (Day & Taylor, 2003; Leimar, 2001). In order to obtain the derivative of $\lambda(\mathbf{x}^\circ, \mathbf{x}^*)$ with respect to a mutant strategy \mathbf{y} , I use the following equation shown by Taylor and Frank (1996):

$$\left. \frac{\partial \lambda(\mathbf{x}^\circ, \mathbf{x}^*)}{\partial \mathbf{x}^\circ} \right|_{\mathbf{x}^\circ = \mathbf{x}^*} = \mathbf{v}^* \left(\left. \frac{\partial \mathbf{A}(\mathbf{x}^\circ, \mathbf{x}^*)}{\partial \mathbf{x}^\circ} \right|_{\mathbf{x}^\circ = \mathbf{x}^*} \right) \mathbf{u}^* / (\mathbf{v}^* \cdot \mathbf{u}^*), \quad (2A.3)$$

where \mathbf{v}^* and \mathbf{u}^* are derived from the resident matrix $\mathbf{A}^*(\mathbf{x}^*, \mathbf{x}^*)$. Assuming that there is no genetic correlation between each trait value x_i , and reflecting equations 2.2 and

2A.3, I obtain the vector of the derivative of $\lambda(\mathbf{x}^\circ, \mathbf{x}^*)$ with respect to a mutant strategy \mathbf{y} and evaluate at $\mathbf{x}^\circ = \mathbf{x}^*$:

$$\left. \frac{\partial \lambda(\mathbf{x}^\circ, \mathbf{x}^*)}{\partial \mathbf{x}^\circ} \right|_{\mathbf{x}^\circ = \mathbf{x}^*} = \left[\left. \frac{\partial \lambda(\mathbf{x}^\circ, \mathbf{x}^*)}{\partial x_i^\circ} \right|_{x_i^\circ = x_i^*} \right] = \left[\left. \frac{u_i v_{i+1} \phi'_i(x_i) + u_p v_p u_i \psi'(E_x^\circ)}{n(1 - \psi(E_x^*)) + 1} \right|_{x_i^\circ = x_i^*} \right], \quad (2A.4)$$

where prime denotes differentiation of a function with respect to its argument and i is from 1 to n .

Let \mathbf{M} be the $n \times n$ Hessian, real symmetric matrix of $\lambda(\mathbf{x}^\circ, \mathbf{x}^*)$, with elements

$$\mathbf{M}_{ij} = \left. \frac{\partial^2 \lambda(\mathbf{x}^\circ, \mathbf{x}^*)}{\partial x_i^\circ \partial x_j^\circ} \right|_{\mathbf{x}^\circ = \mathbf{x}^*}. \quad (2A.5)$$

In order for \mathbf{M} to be negative semi-definite at the equilibrium point (x_1^*, \dots, x_n^*) , $\mathbf{z}^T \mathbf{M} \mathbf{z}$ should be zero or negative for all nonzero vectors \mathbf{z} . Recall that an age- i offspring survival $\phi_i(x_i)$ was assumed to increase with the amount of resources provided, with diminishing returns: $\partial^2 \phi_i(x_i) / \partial x_i^2 < 0$. No genetic correlation was assumed among each different-aged offspring's resource share: $\partial^2 \phi_i(x_i) / \partial x_i \partial x_j = 0$, where $i \neq j$. Moreover, the parent's residual survival was assumed to be a decreasing, concave-down function of current total expenditure: $\partial^2 \psi(E_x) / \partial E_x^2 < 0$. Taking these into account, one can see that $\mathbf{z}^T \mathbf{M} \mathbf{z}$ is zero or negative for all nonzero vectors \mathbf{z} . Therefore, the function $\lambda(\mathbf{x}, \mathbf{x}^*)$ has a local maximum at the equilibrium point $(x_1^*, x_2^*, \dots, x_n^*)$. Note that the same result is obtained even when the parent's residual survival is assumed to linearly decrease with the current total expenditure.

Another stability criterion called convergence stability ensures the evolutionary attainability through a series of small steps (Eshel, 1983; Eshel & Motro, 1981). Denote by $\hat{\mathbf{x}}$ ($= \varepsilon \mathbf{x}^\circ + (1 - \varepsilon) \mathbf{x}^*$) the mean of parental allocation strategy in a population with a rare mutant \mathbf{x}° at frequency ε and the ES strategy \mathbf{x}^* at frequency $(1 - \varepsilon)$ with ε being small. Multidimensional convergence stability requires that the so-called Jacobian matrix of selection gradient, with elements

$$\mathbf{J}_{ij} = \frac{\partial}{\partial \hat{x}_j} \left(\frac{\partial \lambda(\mathbf{x}^\circ, \mathbf{x}^*)}{\partial x_i^\circ} \Big|_{\mathbf{x}^\circ = \hat{\mathbf{x}}} \right) \Big|_{\hat{\mathbf{x}} = \mathbf{x}^*}, \quad (2A.6)$$

be negative definite at the equilibrium point (x_1^*, \dots, x_n^*) (Leimar, 2005; Otto & Day, 2007). The negative definiteness can be checked in the same manner as above; hence the equilibrium point (x_1^*, \dots, x_n^*) is convergence stable.

2.3. The pattern of ES allocation when $\varphi'_i(x) > \varphi'_{i+1}(x)$ for all positive x

Equation 2.8 reveals that δ can be regarded as a function of x_{i+1}^* only. Differentiating $\delta(x_{i+1}^*)$ with respect to x_{i+1}^* , we obtain the following:

$$\frac{\partial}{\partial x_{i+1}^*} \delta(x_{i+1}^*) = \frac{\varphi_{i+1}(x_{i+1}^*) (\varphi''_{i+1}(x_{i+1}^*) - \varphi'_i(x_{i+1}^*) \varphi_{i+1}(x_{i+1}^*)) - (\varphi'_{i+1}(x_{i+1}^*))^2}{(\varphi_{i+1}(x_{i+1}^*))^2} < 0, \quad (2A.7)$$

which means that $\delta(x_{i+1}^*)$ is a decreasing function of x_{i+1}^* .

Since the survival probability must lie in between 0 and 1, I assume that $\varphi_i(x)$ approaches an asymptote of K_i and $\varphi_{i+1}(x)$ approaches K_{i+1} as x approaches infinity ($0 < K_{i+1} < K_i \leq 1$, because $\varphi'_i(x) > \varphi'_{i+1}(x)$ for all positive x). In other words, both $\varphi'_i(x)$ and $\varphi'_{i+1}(x)$ approaches zero as x approaches infinity, which implies that $\delta(x_{i+1}^*)$ approaches zero as x_{i+1}^* approaches infinity. Since $\delta(x_{i+1}^*)$ is a decreasing function of x_{i+1}^* , $\delta(x_{i+1}^*)$ has a positive value for all x_{i+1}^* . Thus x_i^* is lower than x_{i+1}^* for all x_{i+1}^* .

2.4. The pattern of ES allocation when $\varphi'_i(x) > \varphi'_{i+1}(x)$ only for small values of x

Denote by \tilde{x} the specific value of x at which $\varphi'_{i+1}(x)$ becomes equal to $\varphi'_i(x)$. That is, $\varphi'_i(x) > \varphi'_{i+1}(x)$ for $x < \tilde{x}$ but $\varphi'_i(x) < \varphi'_{i+1}(x)$ for $x > \tilde{x}$. First, consider x_{i+1}^* the value of which is greater than \tilde{x} . Given that $\varphi_i(x_{i+1}^*) > \varphi_{i+1}(x_{i+1}^*)$ and $\varphi'_i(x_{i+1}^*) < \varphi'_{i+1}(x_{i+1}^*)$, we can derive the following inequality:

$$\delta = \frac{\varphi'_{i+1}(x_{i+1}^*)}{\varphi_{i+1}(x_{i+1}^*)} - \varphi'_i(x_{i+1}^*) > \frac{\varphi'_{i+1}(x_{i+1}^*)}{\varphi_{i+1}(x_{i+1}^*)} - \frac{\varphi'_i(x_{i+1}^*)}{\varphi_i(x_{i+1}^*)} > 0. \quad (2A.8)$$

Hence x_i^* is lower than x_{i+1}^* for $x_{i+1}^* > \tilde{x}$.

Second, consider x_{i+1}^* the value of which is less than or equal to \tilde{x} . The decreasing function $\delta(x_{i+1}^*)$ has its minimum value at $x_{i+1}^* = \tilde{x}$. The minimum value is positive as follows:

$$\delta(\tilde{x}) = \frac{\varphi'_{i+1}(\tilde{x})}{\varphi_{i+1}(\tilde{x})} - \varphi'_i(\tilde{x}) = \frac{\varphi'_{i+1}(\tilde{x})}{\varphi_{i+1}(\tilde{x})} - \varphi'_{i+1}(\tilde{x}) > 0 \quad (2A.9)$$

Hence $\delta(x_{i+1}^*)$ is positive, which means that x_i^* is lower than x_{i+1}^* for $x_{i+1}^* \leq \tilde{x}$.

In sum, x_i^* is lower than x_{i+1}^* for all x_{i+1}^* .

Chapter 3: Parental Resource Allocation in Humans: An Empirical Test of Competing Evolutionary Hypotheses

SUMMARY

How do parents allocate their limited resources among different children? Darwinian perspective suggests that natural selection has favored discriminative parental psychology that makes unequal distribution of parental resources among offspring in a way that maximizes parental fitness. A few evolutionary hypotheses of human parental favoritism based on offspring birth order thus far have been suggested: Sulloway's (1996: 2001) family dynamics model, Hertwig, Davis, and Sulloway's (2002) equity heuristic model, and Jeon's (chapter 2) game-theoretic model. This study empirically tested the competing predictions derived from each hypothesis, by asking human parents to hypothetically allocate tangible resources like food and money among children. Participants allocated more resources to the older children than the younger children, confirming the predictions of Jeon's game-theoretic model. Neither family dynamics model nor equity heuristic model was empirically validated. The functional organization of psychological adaptations for allocating parental resources among different children is discussed.

INTRODUCTION

One of the unique characteristics in the human family is that immature offspring have a very long developmental period, relative to other primates, and are highly dependent on parental caregiving (Geary & Flinn, 2001; Kaplan & Gangestad, 2005). Even after weaning, children continue to require substantial investment in feeding and

protection from their parents. Since offspring in a family may differ in their general qualities such as age, sex, size, and physical health, parents might make unequal distribution of parental resources among their offspring. Indeed, traditional psychologists have long recognized that parents often treat their children differently, demonstrating that parental favoritism is linked to a problem in the social and emotional development of children (e.g., Brody, Stoneman, & Burke, 1987; Dunn, Stocker, & Plomin, 1990; Stocker, Dunn, & Plomin, 1989). It has remained unexplored, however, how parents are expected to divide their resources among various offspring.

An evolutionary perspective can provide the theoretical framework for analyzing parental psychology. Natural selection may have shaped discriminative mechanisms of parental care that unequally distribute parental resources among various offspring so as to maximize parental fitness (Daly & Wilson, 1988a; Daly & Wilson, 1995; Salmon, 2005; C. C. Smith & Fretwell, 1974; Winkler, 1987). Among many factors affecting the distribution pattern of parental resources, offspring age is of special concern for family researchers because offspring age is correlated with sibling differences in size, power, experience, and status within the family. Unfortunately, how a parent should allocate its resources among its senior and junior offspring has been considered a vexing problem for theoretical biologists, due to mutually counteracting effects of offspring growth on parental investment (PI) (Clutton-Brock, 1991, see chapter 2). The younger or smaller of two offspring may benefit more from an (infinitesimally small) unit of additional food, in terms of its increased survival probability. In other words, the younger offspring has higher needs for food than the older offspring (Sargent & Gross, 1986). However, the older or bigger offspring is closer to reproductive maturity and hence has higher reproductive value, i.e., greater genetic contribution far into the future generations (Fisher, 1930), than the younger offspring. Since it seemed that both the older and younger offspring may have reasonable reason to be favored by parents,

evolutionary psychologists in earlier eras have failed to give a conclusive answer for which offspring would be favored (Daly & Wilson, 1988b; Daly & Wilson, 1995).

Recently, several evolutionary hypotheses of parental resource allocation in humans have been suggested. First of all, in his family dynamics model of birth order effects, Sullo way (1996; 2001) suggested that parents would preferentially invest in both their firstborns and lastborns, while relatively neglecting their middleborns. It appears that Sullo way (1996; 2001) simply combined the two counteracting effects of offspring growth on parental decision rules — reproductive value favors the elder and the impact of additional resources on offspring survival (‘neediness’) favors the younger (Daly & Wilson, 1995) — and predicted a U-shaped pattern of parental resource distribution over offspring birth order for sibships of three or more. It is difficult, however, for Sullo way’s (2001) model to make predictions for sibships of two (Rohde et al., 2003; Sullo way, 2001).

Second, Hertwig, Davis, and Sullo way (2002) proposed the ‘equity heuristic’ as parental allocation decision rule, with which parents should attempt to equally divide resources among their children at any given time. They noted that such a motive of equity would still produce inequality in the cumulative amount of PI over the whole caring period, in a way that middleborns would receive fewer cumulative PI than firstborns and lastborns. The counterintuitive implication results from the fact that firstborns and lastborns experience some period as the only child in the family, whereas middleborns always have to share parental resources with other siblings (see Figure 3.1) (Herwig et al., 2002). An equal allocation is predicted for sibships of two, both at any given time and over the entire period of caregiving. The rationale behind the equity heuristic is that a parent is equally related to each of its offspring by 0.5 degree of genetic relatedness (Hamilton, 1964).

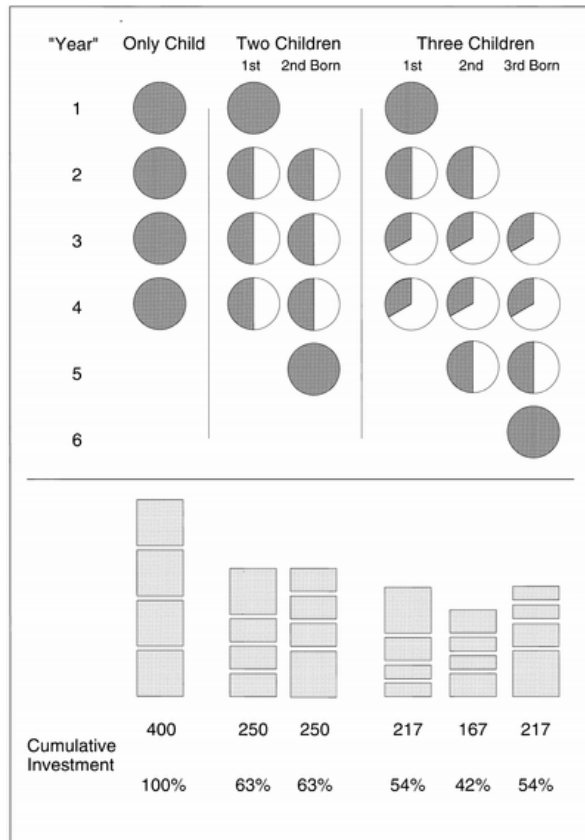


Figure 3.1. A diagram showing how the equity heuristic can result in unequal distribution of cumulative investment among offspring. Spheres in the upper part of the figure represent resource allocation according to the equity heuristic as a function of birth rank in families with one, two, and three children. The bars in the lower part show the absolute and relative (i.e., calculated as a proportion of that for an only child) cumulative investments across four growth periods (“years”).

Source: Herwig, R., Davis, J. N., & Sulloway, F. J. (2002). Parental investment: how an equity motive can produce inequality. *Psychological Bulletin*, 128, 728-745. Reprinted with permission.

Third, in his game-theoretic model of parental resource allocation, Jeon (chapter 1) formally disentangled the two countervailing effects of offspring growth on parental allocation decision. The game-theoretic model determined a parent's evolutionarily stable strategy (ESS), i.e., a strategy such that, if all members of the population adopt it, then no other mutant strategy could invade the population (Maynard Smith & Price, 1973). The parental ESS is to distribute resources such that *the marginal benefits to each offspring, weighted by each offspring's survival probability to the reproducing age, are identical across all offspring*. And then, within the model's reproductive-value framework, the younger offspring's fitness increment with additional resources ('neediness') was assumed to be higher than the older offspring. It was found that, under these circumstances, the parental ESS at a single point in time is to bias parental resources in favor of older offspring: that is, the offspring birth rank will be inversely associated with the amount of resources allocated by parents. Since such a life-history model typically assumes that the respective amounts of PI to the offspring of each age do not change over evolutionary history, the cumulative amounts of PI that each offspring would have received at the end of caring period are identical, irrespective of offspring birth order.

The central aim of the present chapter is to empirically test the competing evolutionary hypotheses of parental favoritism among different-aged children using a questionnaire study of hypothetical allocation. The alternative models make distinct predictions regarding the allocation pattern of parental resources among children at any given point in time (see Table 3.1). Specifically, for sibships of two, Sulloway's (1996; 2001) family dynamics model appears not make any predictions; Hertwig et al.'s (2002) equity heuristic model predicts equal allocation; and Jeon's (chapter 2) game-theoretic model predicts biased allocation toward the older offspring. For sibships of three or more, Sulloway (1996; 2001) predicts U-shaped allocation of resources with the middleborns receiving the least; Hertwig et al. (2002) predicts equal allocation; and

Jeon (chapter 2) predicts biased allocation toward the older offspring. I conducted a survey study in which parents were asked to allocate a certain amount of food among two or three children in hypothetical situations. Although parental investment consists of not a single, tangible resource but qualitatively different kinds of resources (Borgerhoff Mulder, 1998; Herwig et al., 2002), food provisioning may be the most critical component of parental caregiving in many species, including humans. The anatomical features of human childhood, such as an immature dentition (“milk teeth”) and small digestive tracts, strongly suggest that food provisioning has been a recurrent adaptive problem for human parents throughout evolutionary history (Bogin, 1997). Additionally, I performed exploratory studies of parental resource allocation when the resources are time and money.

Table 3.1. A comparison of competing predictions derived from alternative evolutionary hypotheses for parental differential treatment among different-aged children.

	At any given point in time		Cumulative PI at the end of caring period
	Two children	Three or more children	
Family dynamics model	?	U-shaped (middleborns least favored)	U-shaped (middleborns least favored)
Equity heuristics model	Equal	equal	U-shaped (middleborns least favored)
ESS model	unequal (the older favored)	unequal (the older favored)	equal distribution

METHOD

Participants

Participants were approached at a large outdoor park in Austin, Texas, and asked to complete a questionnaire. We recruited only adults having at least two genetic children. A total of 109 participants who met the eligibility criteria provided informed consent and participated in the study. Of these, seven participants were excluded from the sample because of incomplete data. The responses of the remaining 102 participants (49 males, 53 females) of ages 22 to 70 years ($M = 41.53$, $SD = 10.93$) were analyzed. Upon completion, participants were thanked for their participation and debriefed. All participants were volunteers and received no compensation.

Materials and Procedure

Participants first provided demographic information (age, sex, ethnicity, and socioeconomic status). They were instructed to allocate three qualitatively different types of parental investment (food, time, and money, which were counterbalanced in random orders) to their hypothetical two/three children. For two children scenario, participants were asked to imagine that the younger child was a 3-year-old child and the older was 7-year-old child. The procedures was to reflect the fact that the world-wide median age of weaning is reported as 36 months after birth (Dettwyler, 1995). For three children scenario, the firstborn was 9-year-old, the middleborn was 6-year-old, and the lastborn was 3-year-old. Participants were advised not to consider the sex of children. In the case of food allocation task, the two children scenario was as follows:

Suppose that you are the parent of two offspring: a 3-year-old child and a 7-year-old child. One evening you came home late and your children seemed to feel very

hungry. Fortunately, there was a vast pot of soup in the refrigerator. The pot of soup was so huge that it could satisfy a lot of children's hunger simultaneously. In order to make your children's late dinner, you took off an appropriate amount of soup from the pot and warmed it up.... Given that the soup you warmed up constitutes 100%, please indicate how you would like to allocate the food among between your older and younger offspring. Make sure that the sum of two percentages is 100.

In the case of time allocation task, participants were asked to imagine that they came home late one evening and found that their two or three children caught a cold. Given that participants had only one hour to take care of their children, but not simultaneously, they were asked 1) to choose which offspring to look after in the first place and 2) to allocate 60 minutes among their two or three children.

In the case of money allocation task, participants were asked to imagine that they had it a rule to allow their two or three children some pocket money every month. Given that participants were going to give 10 dollars to their two or three children this month, they were asked to allocate 10 dollars among their two or three children. Unlike previous allocation tasks, the ages of children age slightly went up to reflect the fact that small children need not money at all. For two children scenario, the younger was 7-year-old child and the older was 10-year-old child. For three children scenario, the firstborn was 11-year-old, the middleborn was 8-year-old, and the lastborn was 5-year-old.

For each allocation task, it was emphasized that each child will never know of other children's share and hence will not complain about the participants' allocation decision. An open-ended question on why participants allocated in that way was additionally administered for each allocation task.

Data analysis

The dependent variable was percentage of parental resources (food, time, and money) allocated to each offspring with a specific birth order. Although it is generally useful to transform such proportion data by using arcsine or logit transformations, these transformations tend to have little effect if most or all of the proportion data values are between about .2 and .8 (Judd & McClelland, 1989, pp. 525-526), which is the case of my data. The analyses were therefore done on untransformed data. It was confirmed that transformed data using arcsine transformation yield identical results.

Participants' responses to open-ended questions were coded independently by two trained, research assistants. The inter-rater agreements for each allocation task were 95 percent (food), 94 percent (time), and 89 percent (money). Any disagreements between coders were resolved by the investigator.

RESULTS

Preliminary analyses of each allocation task did not find any significant main effects or interactions for the sex of participants ($ps > .05$). Therefore, the data were collapsed across male and female participants in subsequent analyses.

Food allocation task

A repeated measures ANOVA on the percentage of food allocated to each child was conducted for the two children scenario. Consistent with the predictions of Jeon's (chapter 2) game-theoretic model, participants allocated significantly more food to the older child ($M = 61.57$) than the younger child ($M = 38.43$), $F(1, 101) = 195.51$, $p < 0.001$ (see Figure 3.2a). By contrast, the equal allocation prediction derived from Hertwig et al.'s (2002) equity heuristic model was not met. A repeated measures ANCOVA with participants' age as the covariate showed that the difference between

the older child's food share and the younger child's food share was still significant after controlling for the effect of participants' age, $F(1, 100) = 15.54, p < 0.001$. Table 3.2 summarizes the allocation of parental resources among children across all types of resources investigated in this study.

Table 3.2. Percentages of various kinds of parental resources allocated to each offspring according to offspring birth order.

	Types of parental resources					
	Food		Time		Money	
	Mean	SD	Mean	SD	Mean	SD
Two children						
1 st	61.57	8.36	45.10	9.48	56.76	12.99
2 nd	38.43	8.36	55.56	10.25	42.25	12.42
Three children						
1 st	43.65	7.51	28.01	7.86	48.02	12.41
2 nd	32.58	4.15	31.47	4.37	33.73	7.97
3 rd	23.77	6.50	40.36	9.10	18.44	10.95

Similar analyses were performed for three children scenario. The effect of offspring birth order (i.e., offspring's relative age) on the proportion of food allocated was significant, $F(2, 202) = 175.72, p < 0.001$, revealing a significant linear trend, $F(1, 101) = 223.79, p < 0.001$. Pairwise comparison tests using the Bonferroni correction revealed that participants allocated the most food to the firstborn ($M = 43.65$), followed by the middleborn ($M = 32.58$), and finally the lastborn ($M = 23.77$), all pairwise $ps < 0.001$ (Figure 3.2b). Therefore, Jeon's (chapter 2) game-theoretic model that predicts

biased allocation of parental resources in favor of older children was confirmed by the empirical data. Neither Sulloway's (1996; 2001) model predicting U-shaped distribution nor Hertwig et al.'s (2002) model predicting equal allocation was confirmed. The biased allocation pattern toward older children was not influenced by participants' age (repeated measures ANCOVA with participants' age as the covariate, $F(2, 200) = 19.786, p < 0.001$).

Participants' responses to the open-ended question about why they allocated in that way were content analyzed. Since the responses to both two children scenario and three children scenario were nearly identical, only the data for two children scenario are presented here. For participants ($n = 73$) who allocated more food to the older child, their responses were classified into three categories: (1) nutrients requirement (55%) (e.g., "The older has a bigger stomach (appetite)" and "The older needs more calories"); (2) difference in demands (42%) (e.g., "The older needs more food" and "The younger needs less food"); (3) and others (3%) (e.g., "I will know how much each offspring will eat"). Note that (1) and (2) can be lumped together because both invokes age-specific demands. For participants ($N = 17$) who made equal allocation, their responses were classified into three categories: (1) fairness (53%) (e.g., "To show equal love and care" and "To be fair"); (2) the irrelevance of age (24%) (e.g., "The appetite cannot be measured by age"); and (3) others (24%) (e.g., "I don't know who has a bigger appetite"). Not all participants responded to the open-ended question; thus the total number of responses analyzed is less than 102.

(a)



(b)

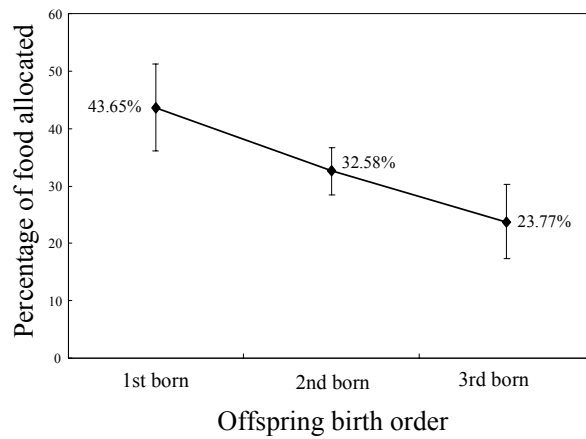


Figure 3.2. Percentages of food allocated with regard to offspring birth order. (a) two children scenario. (b) three children scenario.

Time allocation task

To examine the effect of offspring birth order on the percentage of time allocated to each offspring, a repeated measures ANOVA was conducted for two children scenario. Participants allocated significantly more time to the younger child ($M = 55.56$) than to the older child ($M = 45.10$), $F(1, 101) = 32.23$, $p < 0.001$. The biased allocation

favoring the younger child was not dependent upon participants' age (repeated measures ANCOVA, $F(1, 100) = 4.307, p < 0.05$). Among the participants ($n = 90$) who responded to the question about which offspring to look after in the first place, 88% of them chose the younger child and 10% chose the older child. Therefore, contrary to the previous food allocation task, participants invested more time to the younger child, a phenomenon that is not easily explained by any of the competing hypotheses of parental resource allocation. When the resource to be distributed at a certain point is time, Hertwig et al.'s (2002) model explicitly predicts equal allocation of time. Jeon's (chapter 2) model is primarily intended for tangible resources like food; the model is unable to make predictions for child-care time unless how offspring survival depends on child-care time is specifically determined.

For the three children scenario, the percentages of time allocated were significant different across offspring birth order (repeated measures ANOVA, $F(2, 202) = 51.407, p < 0.001$), showing a significant linear trend, $F(1, 101) = 58.279, p < 0.001$. Pairwise comparisons with the Bonferroni adjustment revealed that participants allocated the most time to the lastborn ($M = 40.36$), followed by the middleborn ($M = 31.47$), and finally the firstborn ($M = 28.01$), all pairwise $ps < 0.001$. The observed pattern of biased allocation in favor of younger children is not consistent with any of the competing evolutionary hypotheses.

Participants' responses to the open-ended question about why they allocated in that way in two children scenario were content analyzed. For participants ($n = 34$) who allocated more time to the younger child, the responses were categorized: vulnerability (59%) (e.g., "The younger is more vulnerable" and "The younger has lower immune system"); the inability to take care of oneself (32%) (e.g., "The younger is less likely to take care of herself"); and others (9%). For participants ($n = 44$) who allocated equally, the responses were classified: (1) fairness (64%) (e.g., "Both are equally important to me" and "Both are my children"); (2) identical needs (30%) (e.g., "Both needs equal

care”); and others (7%). The number of participants ($n = 7$) who allocate more time to the older child was very small.

Money allocation task

For two children scenario, repeated measures ANOVA revealed a significant main effect of birth order on the percentage of money allocated to each child, $F(1, 101) = 39.203, p < 0.001$. Participants allocated significantly more money to the older child ($M = 56.76$) than the younger child ($M = 42.25$). The biased allocation favoring the older was also observed for three children scenario. There was a significant main effect of birth order on the money allocated (repeated measures ANOVA, $F(2, 202) = 132.558, p < 0.001$), showing a significant linear trend, $F(1, 101) = 184.503, p < 0.001$. Pairwise comparison tests showed that participants allocated the most money to the firstborn ($M = 48.02$), followed by the middleborn ($M = 33.73$), and the firstborn ($M = 18.44$), all pairwise $ps < 0.001$. The observed allocation pattern of favoring the older is consistent with predictions from Jeon’s (chapter 2) game-theoretic model. It needs to be established, however, how parental psychological mechanism of allocating evolutionarily relevant resources would operate on the allocation of money, a recent invention that emerged only 3,000 years or so (Davies, 2002).

DISCUSSION

In hypothetically allocating tangible resources like food and money at a single point in time, participants allocated more resources to the older children than the younger children, both for sibships of two and for sibships of three. The results confirmed the prediction of Jeon's (chapter 2) game-theoretic model: offspring birth rank will be inversely associated with the amount of resources allocated by the parent. Neither the prediction of Sulloway's (2001) family dynamics model nor that of Hertwig et al.'s (2002) equity heuristic model has been empirically validated. In allocating child-care time at a single moment, however, participants allocated more time to the younger children than the older children, a phenomenon that has not been predicted by any of the competing evolutionary hypotheses.

Alternative hypotheses of parental investment allocation in humans

Among the evolutionary hypotheses of parental resource allocation in humans, Sulloway's (1996; 2001) family dynamics model has received the greatest attention and stimulated a number of empirical studies (e.g., Rohde et al., 2003; Salmon, 1999; Salmon & Daly, 1998). Sulloway's (1996, 2001) model is, in reality, a grand theory of personality and development that stresses the critical role of birth order in shaping individual differences. The unequal allocation of parental resources is presented in his model as one of the four causal mechanisms resulting in personality differences (note that whether birth order influences personality is not the concern of this paper).

As already described, based on the two counteracting effects of offspring growth on parental allocation decision — reproductive value and the impact of additional resources on offspring survival ('neediness') —, Sulloway (1996, 2001) concluded that parents will invest the least amount of resources in middleborns. Unfortunately, no justification was provided for why reproductive value and 'neediness' are expected to

affect parental allocation decision *independently with each other*. The main finding of this study, parental favoring of older children regarding tangible resources, shows that it should be formally checked, rather than intuitively derived, how reproductive value and ‘neediness’ could have interacted to impose selection pressures on discriminative parental psychology over evolutionary past.

More precisely, the reproductive value of each offspring should *not* be regarded as one of many factors influencing the fitness benefits to the parental actor: it is a common currency, like genetic relatedness, to properly value the fitness benefits derived from each offspring (recipients) to the parental actor (Fisher, 1930; Frank, 1998; Taylor, 1990). With such a reproductive value weighting, Jeon’s (chapter 2) formal model demonstrated that the parental ESS is to equalize the marginal benefits of additional resources (‘neediness’) to each offspring, weighted by the survival probability to the adult age. Note that the survival probability to the adult age is, by definition, is lower for the younger offspring. The model thus has the surprising implication that, after a parent has made adaptive allocation of resources to maximize parental fitness, the younger offspring would be ‘needier’ than the older offspring (though the magnitudes of ‘neediness’ must have been greatly reduced for both, as the result of parental provisioning). Subsequently, assuming that the younger has a higher need for food than the older before the onset of parental provisioning, the model predicts biased allocation in favor of older offspring for both sibships of two and three. The empirical results gained in this study unequivocally support Jeon’s (chapter 2) game-theoretic model, which suggests that formal evolutionary modeling can be very helpful in discovering the nature of evolved psychological mechanisms such as resource allocation module among different children.

In addition to the impact of a unit of additional resources on offspring survival, another factor that will lead parents to favor the younger children (particularly the lastborn) has been seriously considered by some researchers adopting Sulloway’s

(1996; 2001) framework (e.g., Salmon, 1999; Salmon & Daly, 1998). As parents themselves grow older, their residual survival probability decreases due to senescence, favoring parental investment into current offspring. Hence parental aging may have a beneficial effect on the lastborns who are likely to have older parents; this effect will reinforce the U-shaped pattern of resource distribution as Sulloway (1996; 2001) predicted. The effect of parental aging on parental resource allocation will be salient in cumulative PI allocation over the whole caring period, rather than PI allocation at a certain moment in time. Since this study tested how human parents would allocate their resources among children at a given time, whether parental aging would influence the cumulative PI allocation as Salmon and Daly (1998) suggested still remains to be an open question. Given that Jeon's (chapter 2) formal model did not take into account the role of parental aging, future work may explore whether Jeon's (chapter 2) model can be accommodated to include the role of parental aging in shaping cumulative PI allocation pattern.

Contrary to Hertwig et al.'s (2002) hypothesis that human parents with enough resources may use a decision rule that divides parental investment equally among all of their children, the participants in this study who had an unlimited amount of hypothetical food to be allocated made unequal distribution in favor of the older children (see Fig. 3.2). To be fair, Hertwig et al. (2002) made clear that their aim was not to insist that parents are strictly egalitarian no matter what their children's age-specific qualities or demands, but to highlight the overlooked possibility that parents who treat children equally may end up biasing investment in terms of the cumulative amount of parental resources at the end of caring period (Hertwig et al., 2002, p. 728). It was not made explicit, however, how parents will find a compromise between the equity heuristic and an alternative heuristic (e.g., an age-specific decision rule). Hertwig et al.'s (2002) primary prediction was, hence, an equal distribution of resources among children at a given point in time, which was not confirmed in this study. This may well

illustrate that, even if it is true that dividing equally requires less information processing and calculation effort than other allocation rules (Messick, 1993), what natural selection ultimately ‘sees’ is not the energy efficiency of a strategy *per se* but the relative fitness of a certain strategy compared to other strategies in ancestral environments.

Notably, the observed biased allocation of child-care time favoring the younger children was not consistent with any of the competing evolutionary hypotheses. This may be especially bad news for Hertwig et al.’s (2002) equity heuristic model, which contends that the equity heuristic works best if parental resources is fairly limited and stable, like time and attention (Herwig et al., 2002, p. 732). The main difficulty in analyzing the result of time allocation task is that, unlike tangible resources like food, how offspring survival probability would specifically increase as a function of child-care time (i.e., the exact shape of offspring survival graph) is largely unknown among evolutionary biologists (Clutton-Brock, 1991). For example, if offspring survival linearly increases with the child-care time and the slope of the linear function is higher for younger offspring, then Jeon’s (chapter 2) game-theoretic model does predict parental favoring of the younger children under reasonable circumstances. The exact shape of offspring survival function with regard to child-care time is, of course, to be determined empirically.

The design of psychological mechanisms for allocating parental resources among children

Some have suggested that the main findings of the present study, parental favoring of the older children in allocating tangible resources like food, can be more parsimoniously explained by a theory invoking age-specific demands (here ‘demands’ refer to the total amount of food that each child requires to be fully satisfied over a meal or a day. The term should be discriminated from the previous term ‘neediness’, the marginal benefit of a small unit of food to offspring survival) (N. Li and G. Holden,

2007, personal communication). Indeed, participants' responses to the open-ended question clearly show that a great majority of those who favored the older child were keenly conscious of the difference in age-specific demands among offspring. This is, however, a proximate-level explanation of how parental resource allocation among different-aged children operates here and now: in allocating food among their children, human parents sensitively react to the cues of age-specific demands. In order to answer why such a parental motivation system has come into existence to control parental behavior and why other possible motivation systems (such as a motive of strict equity) have not evolved, we need an ultimate-level explanation that maps the functional organization of the evolved psychological mechanisms for allocating resources among children onto the statistically recurrent adaptive problems parents historically have faced in maximizing their inclusive fitness.

Here I attempt to map the information-processing architecture of parental resource allocation system. The psychological adaptation was designed to solve the recurrent adaptive problem that how a parent should optimally allocate resources among its different-aged children. Jeon (chapter 2) showed that the parental solution (i.e., parental ESS strategy) is to allocate resources such that the marginal benefits to each offspring, weighted by the survival probability to the adult age; therefore, the function (or 'purpose') of the psychological mechanism for allocating parental resources is to implement the ESS allocation strategy in parental caregiving. It is never implied that parents are aware of the 'purpose'. Rather, just as people are very good at detecting cheaters in social exchange as if they were playing "tit for tat" strategy in iterated prisoner's dilemma game (Axelrod & Hamilton, 1981; Cosmides & Tooby, 1992), human parents are expected to allocate resources among their children in a particular way as if they were deliberately playing the ESS allocation strategy found in Jeon's (chapter 2) model.

Figure 3.3 illustrates a tentative scheme for the design of parental resources allocation system among different-aged children. Although other important attributes of children, such as sex, health, size, and genetic relatedness, will obviously influence parental allocation decision rule, they are beyond the scope of this study and hence their effects are presumed to be held constant. The parental psychological mechanism for allocating resources among children may be activated by specific forms of input, which may include 1) the respective ages of children, 2) the specific shape of offspring's survival curve with regard to a particular type of resources, and 3) the total amount of resources that can be provided to the children at a fitness cost to the parent herself. Under the fairly general assumption that offspring survival probability will linearly increase with the amount of resources provided or non-linearly increase exhibiting diminishing returns, Jeon's (chapter 2) model determined the decision rule of the system (i.e., the ESS allocation strategy of the parents). The decision rule that processes inputs taken into the system may produce different outputs according to the nature of particular inputs. For instance, if the resource to be allocated is food, then the impact of a small unit of food to offspring will be higher for the younger offspring before the onset of food provisioning (i.e., the younger is 'needier'). In such cases, the parental allocation decision rule will produce the outcome that allocates more resources to the older offspring (see Fig. 3). Note that different outputs are possible if different inputs are taken into the psychological mechanism: for example, 1) children may be of the same age (input 1), 2) the type of resources to be allocated may be substantially different from tangible resources like food (input 2, see previous discussion of the result of time allocation), and 3) the amount of available resources may not be sufficient (input 3). In sum, it is suggested that the scheme illustrated in Figure 3.3 may well capture the functional architecture of psychological adaptations dealing with how to allocate resources among different-aged children.

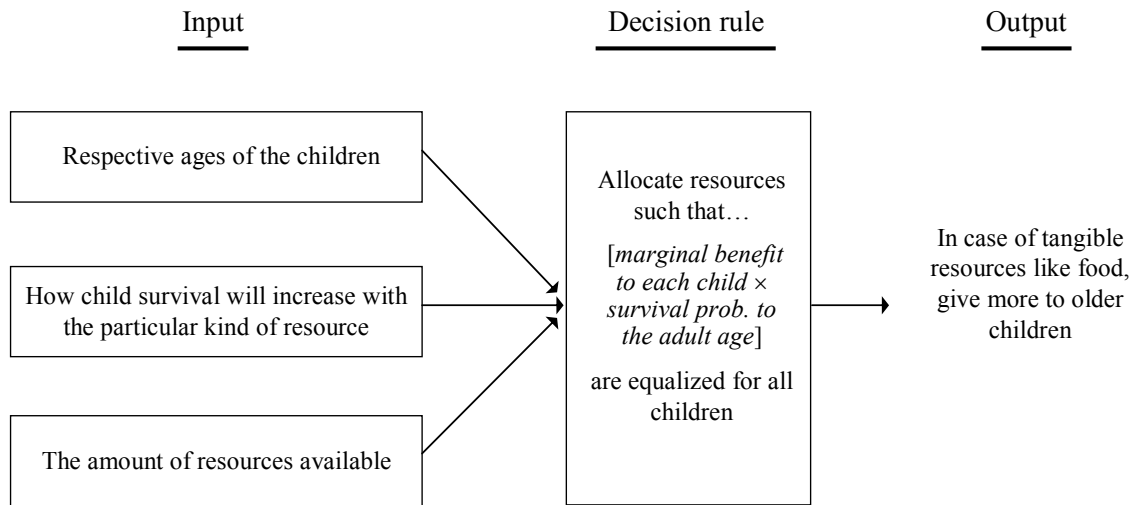


Figure 3.3. A suggested scheme for the functional organization of parental resources allocation system among different-aged children.

Conclusions

Inspired by the fact that the competing evolutionary hypotheses of parental investment allocation among different-aged children make distinct predictions about the allocation pattern at a given point in time, this study attempted to discern which hypothesis successfully predicts participants' responses. The results unequivocally supported Jeon's (chapter 2) game-theoretic model of parental favoritism, which may contribute to fully characterizing the information-processing architecture of discriminative parental psychological mechanisms.

Chapter 4: The Battleground of Intrafamilial Conflict between the Parent, Senior Offspring, and Junior Offspring

SUMMARY

Trivers (1974) first pointed out that family members may be in conflict over the amount of parental investment (PI): each individual offspring favors a preferential investment of PI toward itself whereas parents favor an equal allocation across all offspring. Existing models of intrafamilial conflict tend to separately analyze parent-offspring conflict and sibling competition and do not allow family members to differ in their age. Using an inclusive fitness approach for class-structured populations, I investigate the optimal allocation of PI from the viewpoint of each offspring, and then synthesize the battleground of intrafamilial conflicts between a parent and its multiple offspring of differing ages. If age spacing between siblings is close enough, each offspring favors preferential investment toward itself. Remarkably, if age spacing is distant enough, the junior sibling favors preferential investment of PI toward its senior sibling. Yet the potential for family conflicts is somewhat constantly maintained, because the senior sibling favors far more biased allocation than the junior sibling allows. The results imply that the classic picture of Trivers' (1974) intrafamilial conflict may need to be substantially revised. The current model may provide a useful theoretical framework for inferring the adaptive design of sibling relationships and parental preferential treatment in the human family.

INTRODUCTION

In his seminal paper, Trivers (1974) pointed out that parents and offspring are in conflict over the amount of parent investment (PI). Whereas a parent is equally related to all its progeny, a focal offspring is related to itself twice as much as its full siblings. Thus an offspring is selected to demand more resources than its parent is willing to give. Despite earlier criticisms (Alexander, 1974), the theory of parent-offspring conflict has become one of the key concepts in evolutionary biology and stimulated numerous theoretical and empirical studies of family relations (reviewed in Godfray, 1995a; Mock & Parker, 1997; Parker, Royle, & Hartley, 2002b). Today it is recognized that theoretical models of intrafamilial conflict are classified into two broad categories: 1) battleground models that explore the magnitude of potential genetic conflict by identifying the difference between the optimal distribution of PI for each family member; and 2) resolution models that seek to predict how the potential conflict is actually resolved among family members (Godfray, 1995a, 1999).

Initial models of intrafamilial conflict focused on the case of a single parent investing into a single offspring (e.g., Godfray, 1991; Macnair & Parker, 1978; Parker & Macnair, 1978). They were rather unrealistic, given that most birds and mammals with extensive parental care produce multiple offspring in litters or clutches. Extending the simple model, however, makes it much more difficult to analyze the intrafamilial strife: the actual pattern of PI observed in nature will then be determined by sibling conflict as well as parent-offspring conflict (for simplicity, this paper will not consider the role of sexual conflict between the male and female parents) (Godfray & Johnstone, 2000; Parker et al., 2002b). Many models of PI distribution in larger broods make the simplifying assumption that the total amount of PI delivered to the brood is fixed; thus sibling competition is assumed to influence only the division of PI among offspring, who may differ in their competitive abilities or cryptic internal conditions (i.e., “needs”) (Godfray, 1995b; Parker et al., 1989; Parker et al., 2002a). Clearly, the assumption is

dubious that increased demand by one offspring only reduces the amount of PI available for the other offspring, but does not affect at all parents' future survival and reproduction. Models allowing the total amount of PI to evolve as well typically give parents full control over the total PI amount and thus pay little attention to identifying the ideal distribution of PI from the viewpoint of each individual offspring (Johnstone, 2004; Rodriguez-Girones, 1999; Rodriguez-Girones, Enquist, & Lachmann, 2001).

Offspring within a brood may differ not only in their competitive abilities or cryptic conditions but in some fundamental attributes such as age and sex. In asynchronously hatching birds and most mammals, it is well known that age differences among siblings greatly influence the pattern of food allocation among siblings, resulting in the higher mortality of younger siblings (It is important to note that age discrepancy among siblings should be distinguished from competitive asymmetries. For one, the age differences at earlier ages bring about a number of physiological and developmental changes, not all of which are translated into competitive asymmetries) (Glasse & Forbes, 2002; Magrath, 1990). Despite the marked effect of age differences among offspring on the allocation of PI within the family, it has yet to be analyzed how intrafamilial conflict among a parent and its multiple offspring of differing ages takes place.

Consider the simplistic case of a single parent looking after its two offspring of differing ages. The parent will have its own view of how much PI to deliver and how to divide the PI among the two offspring. Meanwhile, each offspring will also have its own view of how much resource the parent should invest in its sibling, as well as in it (see Figure 4.1). According to Trivers' (1974) classical theory of parent-offspring conflict, each offspring will obviously want more resources for itself than the parent wants to give. But *how much PI would each offspring 'want' the parent to invest in its sibling?* Verbal reasoning based on only genetic relatedness does not seem to help much here, because in most cases a focal offspring will be equally related to both its sibling

and the parent. Given that the parent is close to death and may need to increase its reproductive effort anyhow, a focal offspring may want the parent to invest a lot in its sibling. However, given that the two young are fiercely competing for limited parental resources, a focal offspring may want the parent to invest little in its sibling. Hence the question seems insurmountable. At the very least, since a focal offspring is twice as closely related to itself as to its sibling, it could be safely argued that a focal offspring would “want his mother to invest in him more than in any particular brother or sister” (Dawkins, 1976, p. 128). As we shall see later, even this fairly straightforward argument does not always hold true.

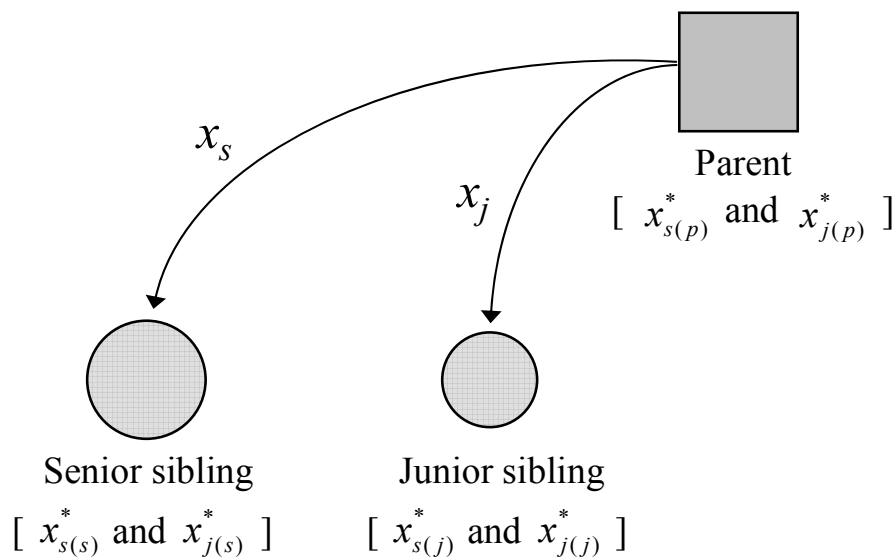


Figure 4.1. A diagram for intrafamilial conflict over the allocation of parental resources among two offspring of differing ages. Each family member (a parent, the senior sibling, and the junior sibling) has different evolutionary interests concerning the amount of parental resources that each of the two offspring should obtain. Here $x_{s(j)}^*$ indicates, for example, the optimal resource share of the senior offspring from the perspective of the junior offspring.

Also, $x_{s(p)}^*$ indicates the optimal resource share of the senior from the perspective of the parent.

In order to construct a battleground model for intrafamilial conflict among a parent and its different-aged offspring, we should take into account two counteracting effects of offspring growth on the allocation of PI. Take, for example, the perspective of the parent. It might pay the parent to bias its resources toward its senior offspring, because senior offspring have higher reproductive value, i.e., greater genetic contribution far into the future generation (Fisher, 1930). However, it might also pay the parent to bias its resources toward junior offspring, because they could benefit more from additional resources than their senior offspring, in terms of increased survival probability (Clutton-Brock, 1991; Rubenstein, 1982; Sargent & Gross, 1986). The same dilemma can be said for the perspective of each offspring, which complicates the mapping of intrafamilial conflict.

In this paper, I investigate the conflict battleground among a parent and its offspring of differing ages. Using an inclusive fitness approach (Taylor, 1990, 1996), I develop kin selection models of class-structured populations in which individuals fall into different age classes. The optimal allocation of PI among different-aged offspring from the perspective of the parent was explored elsewhere (chapter 2). Here I identify the optimal allocation of PI from the perspective of each different-aged offspring and then construct the battleground of intrafamilial conflict when offspring differ in their ages. The model shows that a focal offspring's ideal resource shares from the perspective of each family member (the parent, the focal offspring itself, and the siblings) never coincide, which implies a wide variety of family conflicts even in a simplistic family system. Surprisingly, contrary to Dawkins' (1976) expectations, a focal offspring may 'want' the parent to invest less resource in it than in its sibling(s) under certain circumstances.

THE MODEL

Population structure and life history

Consider a hermaphroditic population that is structured into $n + 1$ age classes, that is, a parental class (class P) and n offspring classes (class O_i : $i = 1, \dots, n$). The population is also subdivided into distinct broods: each parent provisions only their own offspring within its brood. After mating with another adult, a single parent produces $2f$ newborn offspring per each time step. The parent actually expects fitness credit for f offspring since one-half of the newborn offspring are credited to its mate.

The time step in this system corresponds to the average age gap between siblings; it will be measured in days for asynchronously hatching birds and in months or years for mammals (The model thus focuses on within-year dynamics for the case of birds). For simplicity, I do not take into account the dynamic (i.e., time-dependent) aspects of parent-offspring interactions. Instead I assume that, for each time step, the parent-offspring interaction is composed of a series of feeding events and that the outcome of each event has an independent effect on the genetic success of an allocation strategy.

During each time step, a parent distributes its limited resources among its different-aged offspring at a cost of the parent's residual survival. Since there may be a multiple number of offspring within the same age class, we denote by u_i the average number of age- i offspring per each adult. Let x_i be the amount of PI that a single age- i offspring receives by its parent. Therefore, the total amount of PI that a parent invests in its current entire offspring per time step is denoted as $E_x = \sum_i u_i x_i$. The parent's allocation pattern among its offspring of n age classes is described by a vector $\mathbf{x} = [x_1, x_2, \dots, x_n]$, where each trait value x_i is determined by distinct genes and the n traits are genetically uncorrelated with each other. It takes n time steps for a newborn offspring of age-1 to survive and grows into a reproducing adult: an age- i offspring survives into the next time step with survival probability $\varphi_i = \varphi_i(x_i)$, an increasing function of the amount of PI

it receives from the parent. The parent survives to the next time step with probability $\psi = \psi(E_x)$, a decreasing function of E_x .

To determine the conflict battleground within the family, the model developed here seeks the optimal allocation of PI from the viewpoint of offspring in a certain age class (the optimal allocation from the viewpoint of the parent was given in chapter 2). I assume that offspring in age- k ($k = 1, \dots, n$) class have complete control over both how much PI in total should be delivered and how the PI should be divided among the different-aged offspring. That is, the allocation strategy \mathbf{x} is solely determined by the genes expressed within the body of age- k offspring. The dynamics of the resident population is given by $\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$, where $\mathbf{n}(t) = [n_1, n_2, \dots, n_n, n_p]$ indicates the number of offspring in age classes from 1 to n and that of parents at time t . The population transition matrix \mathbf{A} is

$$\mathbf{A} = \begin{bmatrix} 0 & \dots & 0 & \dots & 0 & f \\ \varphi_1(x_1) & \dots & 0 & \dots & 0 & 0 \\ \vdots & \ddots & 0 & \dots & 0 & 0 \\ 0 & 0 & \varphi_k(x_k) & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & 0 & 0 \\ 0 & 0 & 0 & 0 & \varphi_n(x_n) & \psi(E_x) \end{bmatrix}. \quad (4.1)$$

The matrix \mathbf{A} in the ‘normal’ resident population (i.e., harboring no mutant strategy) will eventually reach at demographic equilibrium. Let us denote the normal matrix at equilibrium by \mathbf{A}^* . Assuming zero population growth, the dominant eigenvalue λ of \mathbf{A}^* is 1. The vector of stable age distribution $\mathbf{u}^* = [u_1^*, u_2^*, \dots, u_n^*, u_p^*]$ is the dominant right eigenvector of \mathbf{A}^* ; the vector of individual reproductive value $\mathbf{v}^* = [v_1^*, v_2^*, \dots, v_n^*, v_p^*]$ is the dominant left eigenvector of \mathbf{A}^* (see Supplemental data 1). Since \mathbf{u}^* and \mathbf{v}^* can be scaled at will, I choose the abundance of parental class u_p^* to equal 1, so that u_i^* represents the number of age- i offspring per adult in the normal population.

Inclusive fitness approach

The inclusive fitness approach focuses on a random actor and adds up the effects of its deviant act on the fitness of all recipients; thus it estimates the fitness of a rare, mutant strategy in a normal population (Hamilton, 1964; Taylor, 1990, 1996; Taylor, Wild, & Gardner, 2006). The so-called ‘inclusive fitness effect’, i.e., the difference between the mutant fitness and normal fitness, tells us whether the mutant strategy will be selected or eliminated in the population.

To determine the optimal allocation of PI from the viewpoint of offspring of a certain age, I fasten attention to a focal age- k mutant offspring (the ‘actor’) using a slightly different allocation strategy $\mathbf{x}^\circ = [x_1^\circ, x_2^\circ, \dots, x_n^\circ]$ ($x_i^\circ = x_i + \Delta x$) in the resident population dominated by the normal strategy \mathbf{x} . The mutant strategy is assumed to be rare enough that the number of age- i offspring per adult is still given by u_i^* . The recipients of the focal juvenile actor’s allocation behavior will belong to different age classes: the age- k actor itself, the actor’s different-age siblings, and the parent. First, the focal age- k juvenile actor with the mutant strategy \mathbf{x}° will ‘take’ x_k° resources from the parent. Second, we should calculate the amount of PI that the actor’s different-age sibling should receive, which is rather complicated to obtain. If the brood containing the focal juvenile actor has a multiple number of age- k offspring (the number is u_k^* , including the focal actor), then each of the actor’s different-age siblings should get the average amount of PI allocated by both the focal age- k mutant actor and the $(u_k^* - 1)$ individuals of normal age- k offspring. Consequently, the average amount of PI that a single age- i ($i \neq k$) offspring receive from the parent, denoted as \bar{x}_i , is given by $[x_i^\circ + (u_k^* - 1)x_i]/u_k^*$. If u_k^* is equal to or less than 1, then u_k^* can be interpreted as the probability that the brood will actually contain the focal age- k mutant actor. In this case, a single age- i offspring will get x_i° resources if the brood actually has the focal juvenile actor with probability of u_k^* ; it will get x_i resources if the brood does not have the focal juvenile actor with probability of $(1 - u_k^*)$. Hence \bar{x}_i is given by $u_k^*x_i^\circ +$

$(1-u_k^*)x_i$ when $u_k^* \leq 1$. Finally, the total amount of PI that the focal mutant actor's parent invests in its current brood is denoted as $\bar{E}_x = \sum_i u_i^* \bar{x}_i$. The transition matrix of the mutant subpopulation within the resident population is given by

$$\mathbf{A}(\mathbf{x}^\circ, \mathbf{x}^*) = \begin{bmatrix} 0 & \dots & 0 & \dots & 0 & f \\ \varphi_1(\bar{x}_1) & \dots & 0 & \dots & 0 & 0 \\ \vdots & \ddots & 0 & \dots & 0 & 0 \\ 0 & 0 & \varphi_k(x_k^\circ) & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & 0 & 0 \\ 0 & 0 & 0 & 0 & \varphi_n(\bar{x}_n) & \psi(\bar{E}_x) \end{bmatrix}. \quad (4.2)$$

Let us now identify the fitness of recipients who may belong to different age classes. The fitness of a random individual in a certain class can be given by the sum of its fitness contribution into the next time step, each weighted by the individual class reproductive value (Taylor, 1990; Taylor et al., 2006). Accordingly, the recipient fitness of the focal age- k actor is

$$w_k = v_{k+1} \varphi_k(x_k^\circ) = (\varphi_{k+1}^* \varphi_{k+2}^* \dots \varphi_n^*) \varphi_k(x_k^\circ), \quad (4.3)$$

where v_{n+1} is equal to v_p for $k = n$ (Supplemental data 4.1). The recipient fitness of an age- i ($i \neq k$) offspring (the actor's different-age sibling) is:

$$w_i = v_{i+1} \varphi_i(\bar{x}_i) = (\varphi_{i+1}^* \varphi_{i+2}^* \dots \varphi_n^*) \varphi_i(\bar{x}_i), \quad (4.4)$$

where \bar{x}_i is given by either $[x_i^\circ + (u_k^* - 1)x_i]/u_k^*$ for $u_k^* > 1$ or $u_k^* x_i^\circ + (1 - u_k^*)x_i$ for $u_k^* \leq 1$. The recipient fitness of the focal actor's parent is:

$$w_p = v_1 f + v_p \psi(\bar{E}_x) = \varphi_1^* \varphi_2^* \dots \varphi_n^* f + \psi\left(\sum_i u_i^* \bar{x}_i\right) \quad (4.5)$$

The inclusive fitness effect $\Delta \mathbf{W}$ of the focal age- k actor's deviant allocation strategy \mathbf{x}° is calculated by the sum of the effects of the deviant strategy on the fitness of all recipients, each weighted by the actor's relatedness to the individual recipient. Let r_{ki} be the coefficient of relatedness between the age- k juvenile actor and its age- i sibling; let r_{kp} the relatedness between the age- k actor and its parent. For the focal actor's deviant allocation strategy, one recipient exists in the age- k class (the actor itself), u_i^* recipients exist in the age- i ($i \neq k$) class, and one parent exists in the parental class. The

equilibrium allocation strategy \mathbf{x}^* of a focal age- k juvenile actor is thus determined by letting $\Delta\mathbf{W}$ equal a vector of zeros:

$$\Delta\mathbf{W} = \left[r_{kk} \frac{\partial w_k}{\partial \mathbf{x}^\circ} + \sum_{i \neq k} u_i^* r_{ki} \frac{\partial w_i}{\partial \mathbf{x}^\circ} + r_{kp} \frac{\partial w_p}{\partial \mathbf{x}^\circ} \right]_{\mathbf{x}^\circ = \bar{\mathbf{x}} = \mathbf{x}^*} = \mathbf{0} \quad (4.6)$$

where $\mathbf{0}$ is a vector of zeros. From equation 4.6 and Supplemental data 4.1, the following n equilibrium conditions for are derived:

$$\begin{aligned} r_{k1}(\varphi_2^* \varphi_3^* \dots \varphi_n^*) \varphi_1'(x_1^*) &= -r_{kp} \psi'(E_x^*) \\ r_{k2}(\varphi_3^* \dots \varphi_n^*) \varphi_2'(x_2^*) &= -r_{kp} \psi'(E_x^*) \\ &\vdots \\ (\varphi_{k+1}^* \dots \varphi_n^*) \varphi_k'(x_k^*) &= -r_{kp} \psi'(E_x^*) \\ &\vdots \\ r_{kn} \varphi_n'(x_n^*) &= -r_{kp} \psi'(E_x^*) \end{aligned} \quad (4.7)$$

where the prime denotes differentiation of a function with respect to its argument and $E_x^* = \sum_i u_i^* x_i^*$. We can rewrite equations 4.7 as:

$$r_{k1}(\varphi_2^* \varphi_3^* \dots \varphi_n^*) \varphi_1'(x_1^*) = r_{k2}(\varphi_3^* \dots \varphi_n^*) \varphi_2'(x_2^*) = \dots = (\varphi_{k+1}^* \dots \varphi_n^*) \varphi_k'(x_k^*) = \dots = r_{kn} \varphi_n'(x_n^*) = -r_{kp} \psi'(E_x^*) \quad (4.8)$$

Equation 4.8 shows that an age- k offspring will be selected to allocate PI such that the marginal benefit of additional resources to its own survival $\varphi_k'(x_k^*)$, weighted by its survival probability to the reproducing age $(\varphi_{k+1}^* \dots \varphi_n^*)$, is equal to the relatedness-weighted marginal benefit to its different-age sibling's survival $r_{ki} \varphi_i'(x_i^*)$, weighted by the sibling's survival probability to the reproducing age $(\varphi_i^* \dots \varphi_n^*)$. Moreover, these properly weighted marginal benefits should be balanced by the relatedness-weighted marginal cost of current total investment to the parent's residual survival $r_{kp} \psi'(E_x^*)$. Readers may notice that equation 4.8 is a marginal version of Hamilton's (1964) rule, in which the marginal fitness effects of the focal age- k actor's allocation behavior via direct and indirect routes are scaled by the corresponding coefficient of relatedness (Frank, 1998, 2006).

It should be checked whether the equilibrium allocation strategy $\mathbf{x}^* = [x_1^*, x_2^*, \dots, x_n^*]$ of a focal offspring represents a set of evolutionary attractors that would persist over evolutionary time. This dynamical concept of stability is referred to as ‘dynamically stable strategy (DSS)’ (Wild & Taylor, 2004), which accords with the stability theory of dynamical systems (Leimar, in press). The DSS condition is considered in Supplemental data 4.2.

Thus far, we have concentrated on the optimal allocation of PI from each offspring’s perspective. In order to avoid the confusion caused by the fact that the ideal resource share of a focal offspring may be different according to each family member’s perspectives, I hereafter denote by $x_{i(j)}^*$ the ideal resource share of an age- i offspring from the perspective of an age- j offspring. Similarly, $x_{i(p)}^*$ is denoted as the ideal resource share of an age- i offspring from the parent’s perspective. The optimal allocation of PI from the parent’s perspective is given by the following equilibrium conditions (chapter 2):

$$(\varphi_{2(p)}^* \varphi_{3(p)}^* \dots \varphi_{n(p)}^*) \varphi_1'(x_{1(p)}^*) = (\varphi_{3(p)}^* \dots \varphi_{n(p)}^*) \varphi_2'(x_{2(p)}^*) = \dots = \varphi_n'(x_{n(p)}^*) = -\psi'(E_{x(p)}^*). \quad (4.9)$$

Equation 4.9 means that the parent is selected to allocate PI such that the marginal benefit of additional resources to each offspring’s survival $\varphi_i'(x_{i(p)}^*)$, weighted by the offspring’s survival probability to the reproducing age $(\varphi_{i+1(p)}^* \dots \varphi_{n(p)}^*)$, is all equal to the marginal cost of current total expenditure to the parent’s residual survival $\psi'(E_{x(p)}^*)$. Being obtained by the standard ESS modeling technique, equation 4.9 lacks the relatedness terms between the parental actor and each offspring recipient. To be consistent with the inclusive fitness approach employed in this paper, I use the following equation:

$$r_{p1} (\varphi_{2(p)}^* \varphi_{3(p)}^* \dots \varphi_{n(p)}^*) \varphi_1'(x_{1(p)}^*) = r_{p2} (\varphi_{3(p)}^* \dots \varphi_{n(p)}^*) \varphi_2'(x_{2(p)}^*) = \dots = r_{pn} \varphi_n'(x_{n(p)}^*) = -\psi'(E_{x(p)}^*), \quad (4.10)$$

where r_{pi} the coefficient of relatedness between the parental actor and the age- i offspring recipient. I hereafter assume that $r_{p1} = \dots = r_{pn} = r_p$. Note that equations 4.9 and 4.10 give qualitatively same results on the parental optimal strategy.

RESULTS

How much resource should my sibling receive from our parent?

In this section I derive concrete predictions on the optimal allocation of PI from a focal offspring's perspective. Following previous research, I assume that the impact of additional resources on younger offspring's survival is higher than that on older offspring's survival (Clutton-Brock, 1991; Rubenstein, 1982; Sargent & Gross, 1986; West-Eberhard, 1975). There may be two general situations that we should further consider: (1) a younger offspring may yield higher marginal returns for every level of resources that was already provided during a feeding episode, or 2) a younger offspring may yield higher marginal returns only when the resources already provided are none or few (i.e., only when both are equally hungry); if the resources provided are relatively high (i.e., when both were equally fed well), the marginal gain of extra resources would be higher for the older offspring. It was checked that both situations make qualitatively the same predictions. Therefore this chapter presents only the results under the second situation, which may be more plausible (for detailed explanation, see chapter 2). As before, it is assumed that a focal offspring completely controls both the total amount of PI that is delivered by the parent and how to allocate the PI among itself and other siblings.

What amount of PI would a focal age- k offspring 'allocate' to its siblings, as well as to itself? Recall that the survival probability of an offspring is expected to increase with the resources provided, with diminishing returns (i.e., $\varphi'(x) > 0$, $\varphi''(x) < 0$) (e.g., Smith & Fretwell, 1974). Consider the focal age- k offspring and its younger sibling

aged $k-1$. At evolutionary equilibrium, each sibling will receive the optimal level of resources ($x_{k(k)}^*$ and $x_{k-1(k)}^*$, where $k=2, \dots, n$) from the parent (optimal in the sense that the focal age- k sibling's inclusive fitness is maximized by the specific allocation pattern). Since $\varphi'(x)$ decreases with x , whether $x_{k(k)}^*$ is larger or smaller than $x_{k-1(k)}^*$ can be determined by comparing the younger sibling's marginal return at being given $x_{k-1(k)}^*$ with its marginal return at being given $x_{k(k)}^*$. For instance, if $\varphi'_{k-1}(x_{k-1(k)}^*)$ is larger than $\varphi'_{k-1}(x_{k(k)}^*)$, then $x_{k-1(k)}^*$ will be less than $x_{k(k)}^*$. Meanwhile, equation 4.8 implies the following equation:

$$r_{k,k-1}\varphi_k(x_{k(k)}^*)\varphi'_{k-1}(x_{k-1(k)}^*) = \varphi'_k(x_{k(k)}^*), \quad (4.11)$$

where $r_{k,k-1}$ is the coefficient of relatedness between the focal age- k actor and its age- $(k-1)$ sibling. It is thus obvious that

$$\varphi'_{k-1}(x_{k-1(k)}^*) - \varphi'_{k-1}(x_{k(k)}^*) = \frac{1}{r_{k,k-1}} \frac{\varphi'_k(x_{k(k)}^*)}{\varphi_k(x_{k(k)}^*)} - \varphi'_{k-1}(x_{k(k)}^*) > \frac{\varphi'_k(x_{k(k)}^*)}{\varphi_k(x_{k(k)}^*)} - \varphi'_{k-1}(x_{k(k)}^*). \quad (4.12)$$

The rightmost term in equation 4.12 is always positive; thus, $x_{k-1(k)}^*$ turns out to be less than $x_{k(k)}^*$. From a focal offspring's perspective, the optimal resource share that its younger sibling should get from the parent is less than the optimal resource share that the focal offspring itself should get. In sum, an elder sibling thus will always want its parent to invest more in itself than in its younger sibling.

Let us now consider a focal age- k offspring and its elder sibling aged $k+1$. As in the previous paragraph, each offspring will get the optimal level of resources, $x_{k(k)}^*$ and $x_{k+1(k)}^*$ ($k=1, \dots, n-1$) at evolutionary equilibrium. Whether $x_{k(k)}^*$ is larger or smaller than $x_{k+1(k)}^*$ can be determined by comparing the focal offspring's marginal return at $x_{k(k)}^*$ with its marginal return at $x_{k+1(k)}^*$. That is, the sign of $[\varphi'_k(x_{k(k)}^*) - \varphi'_k(x_{k+1(k)}^*)]$ tells us whether $x_{k(k)}^*$ is larger or smaller than $x_{k+1(k)}^*$. From equation 4.8, it can be derived that

$$\varphi_{k+1}(x_{k+1(k)}^*)\varphi'_k(x_{k(k)}^*) = r_{k,k+1}\varphi'_{k+1}(x_{k+1(k)}^*), \quad (4.13)$$

where $r_{k,k+1}$ is the coefficient of relatedness between the focal age- k actor and its age- $(k+1)$ sibling. It is thus obvious that

$$\varphi'_k(x_{k(k)}^*) - \varphi'_k(x_{k+1(k)}^*) = r_{k,k+1} \frac{\varphi'_{k+1}(x_{k+1(k)}^*)}{\varphi_{k+1}(x_{k+1(k)}^*)} - \varphi'_k(x_{k+1(k)}^*) < \frac{\varphi'_{k+1}(x_{k+1(k)}^*)}{\varphi_{k+1}(x_{k+1(k)}^*)} - \varphi'_k(x_{k+1(k)}^*). \quad (4.14)$$

Since the rightmost term in equation 4.14 is always positive, the sign of $[\varphi'_k(x_{k(k)}^*) - \varphi'_k(x_{k+1(k)}^*)]$ can be positive, negative, or zero, i.e., $x_{k(k)}^*$ can be smaller or larger than, or equal to, $x_{k+1(k)}^*$. Therefore, from a focal offspring's perspective, the optimal resource share that the offspring itself should get from the parent may be larger or smaller than, or equal to, the optimal resource share that its elder sibling should get. Surprisingly, this implies that a younger focal offspring sometimes may 'want' its parent to invest less in itself than in its elder sibling, although the focal offspring is twice as closely related to itself.

To illustrate the above results, I temporarily assume explicit functions for an age- i offspring survival:

$$\varphi_i(x_i) = K[1 - \exp(-c_i x_i)], \quad (4.15)$$

where the shape constant c_i is allowed to vary according to an offspring's distinct age. It was assumed that a younger offspring would yield higher marginal returns only when the resources already provided are none or few. If both offspring are equally fed well, then it would be the older offspring that yields higher marginal returns with additional resources. In order to ensure such a relationship, c_i is assumed to be larger than c_{i+1} . In other words, the shape constant c_i of an age- i offspring survival curve will be inversely related to the offspring's age: $c_1 > c_2 > \dots > c_n$ (Fig. 4. 2) (Sargent & Gross, 1986; Clutton-Brock, 1991). Meanwhile, a parent's residual survival probability is given by an exponentially decreasing function of current parental expenditure (i.e., each increment of parental investment is more costly than the previous increment):

$$\psi(E_x) = G - a \cdot \exp(bE_x) = G - a \cdot \exp\left(b \sum_{i=1}^n u_i^* x_i\right), \quad (4.16)$$

where a and b are positive parameters that specify how the total amount of resources provided to the current brood reduces the parent's residual survival and G is a positive constant.

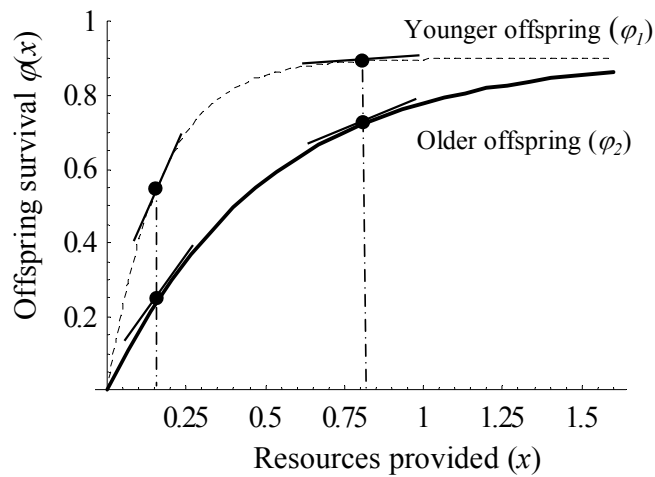


Figure 4.2. The survival probabilities of each offspring ($\varphi(x)$) as a function of the resources provided (x) during a single feeding episode. With a low value of x , the slope of the tangent line to a survival curve at the point $(x, \varphi(x))$, i.e., $\partial\varphi(x)/\partial x$, is higher for the younger offspring's curve φ_1 than the older offspring's curve φ_2 ; when x is relatively high, the slope of the tangent line is higher for the older offspring's curve φ_2 . Parameters are $K = 0.9$, $c_1 = 6$, and $c_2 = 2$.

Figure 4.3a shows the optimal allocation of PI among two different-aged offspring from the perspective of the senior sibling. The graph was plotted across a range of the senior sibling's shape constant c_2 with the junior sibling's constant c_1 being fixed. Given that the shape constant would be inversely related to offspring age, the decrease of c_2 may correspond to the increase of the senior's age with the junior's age being fixed. As expected, it turns out that the senior sibling always 'wants' its parent to invest

more in itself than its junior sibling (Fig. 4.3a). Moreover, the degree of favoring the senior itself increases as the age spacing between the two siblings increases. Figure 4.3b reveals the optimal allocation of PI from the junior sibling. When the age spacing is close enough, the junior sibling ‘wants’ its parent to invest more in itself than its senior sibling. As the age spacing increases, however, the trend becomes reversed: under a sufficiently large age gap, the junior sibling will ‘want’ its parent to invest less in itself than its senior sibling (Fig. 4.3b).

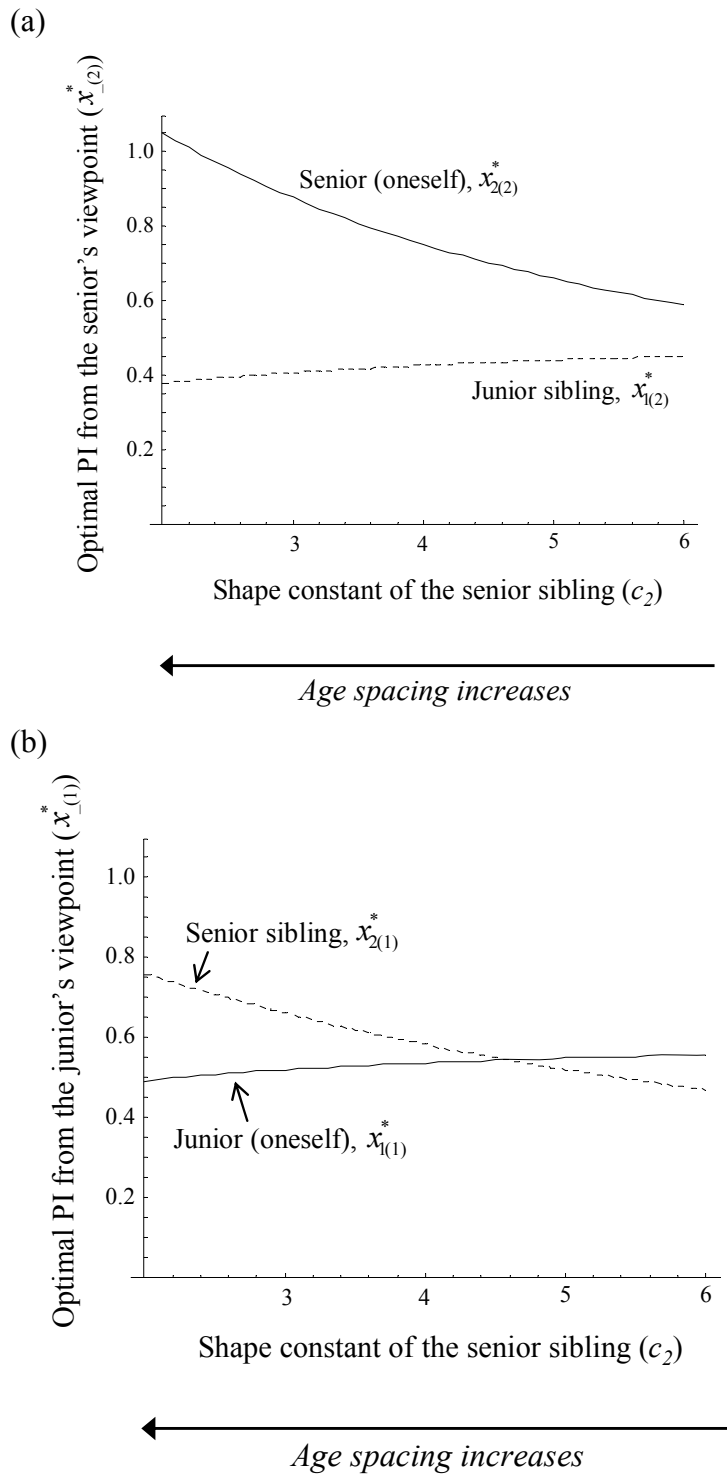


Figure 4.3. The optimal allocation of PI from the viewpoint of each sibling, when the senior sibling's shape constant c_2 is varied from 6 to 2 with the junior sibling's constant c_1 being fixed at 6. As the shape constant will be inversely associated with offspring age, this could be understood as

increasing the senior's age only with the junior's age being fixed. (a) The optimal allocation of PI from the viewpoint of the senior sibling. The equilibrium values were obtained from a variation of equation (8): $r_{21}\varphi_2(x_{2(2)}^*)\varphi_1'(x_{1(2)}^*) = \varphi_2'(x_{2(2)}^*) = -r_{2p}\psi'(E_{x(2)}^*)$, where $E_{x(2)}^* = fx_{1(2)}^* + f\varphi_1(x_{1(2)}^*)x_{2(2)}^*$. (b) The optimal allocation of PI from the viewpoint of the junior sibling. The equilibrium values were obtained from $\varphi_2(x_{2(1)}^*)\varphi_1'(x_{1(1)}^*) = r_{12}\varphi_2'(x_{2(1)}^*) = -r_{1p}\psi'(E_{x(1)}^*)$, where $E_{x(1)}^* = fx_{1(1)}^* + f\varphi_1(x_{1(1)}^*)x_{2(1)}^*$. Parameters used are $K = 0.9, f = 1.2, a = 0.1, b = 1$, and $r_{1p} = r_{12} = r_{2p} = 0.5$.

The battleground of conflicts among family members

Having seen that each family member has different optima for how parental resources should be allocated among offspring, I now attempt to define over what parameter space potential genetic conflict can occur (i.e., to define the 'battleground' of family conflicts). To simplify the matter, I focus on the case of a single parent looking after its two offspring of differing ages.

First, how would family conflicts take place over the amount of resources that should be delivered to an age-1 junior sibling? It is intuitively obvious that the junior's resource share insisted on by the junior itself $x_{1(1)}^*$ would be larger than either the junior's share insisted on by the parent $x_{1(p)}^*$ or the junior's share insisted on by the age-2 senior sibling $x_{1(2)}^*$. Indeed, this can be easily proved and hence its proof shall be omitted. How will the parent and the senior be in conflict over the amount of resources to be delivered to the junior? In order for $x_{1(p)}^*$ to be less than $x_{1(2)}^*$, i.e., for the junior's optimal share from the parental perspective to be less than the junior's optimal share from the senior's perspective, $\varphi_1'(x_{1(p)}^*)$ should be larger than $\varphi_1'(x_{1(2)}^*)$. Based on equations (8) and (10), the condition for $x_{1(p)}^* < x_{1(2)}^*$ can be rearranged as follows:

$$\frac{\psi'(E_{x(p)}^*) \varphi_2(x_{2(2)}^*) r_{21}}{\psi'(E_{x(2)}^*) \varphi_2(x_{2(p)}^*) r_{2p}} > r_p = 0.5. \quad (4.17)$$

It can be easily seen that inequality 4.17 is likely to hold, particularly if the sibling pairs are full siblings. For full-siblings, both the senior's genetic relatedness to the junior r_{21} and the senior's relatedness to the parent r_{2p} are 0.5 and hence r_{21}/r_{2p} can be ignored in inequality (20). Since $\psi'(E_{x(p)}^*)/\psi'(E_{x(2)}^*)$ will be slightly less than unity and $\varphi_2(x_{2(2)}^*)/\varphi_2(x_{2(p)}^*)$ is always larger than unity, the left-hand side of inequality 4.17 will be larger than 0.5 under nearly all circumstances. In short, for full siblings, the junior's optimal resource share insisted on by the parent $x_{1(p)}^*$ will be less than the junior's share insisted on by the senior $x_{1(2)}^*$, unless the marginal cost of current total investment to the parental residual survival drops too abruptly (Interestingly, for half-siblings, inequality 4.17 becomes $[\psi'(E_{x(p)}^*)/\psi'(E_{x(2)}^*)][\varphi_2(x_{2(2)}^*)/\varphi_2(x_{2(p)}^*)] > 1$, which is more difficult to be met. In the case of half-siblings, therefore, it is very likely that the senior sibling, not the parent, would insist on the least amount of resources for the share of the junior sibling).

Next, how do family members disagree about the amount of resources that should be delivered to the age-2 senior sibling? Obviously, the senior's resource share insisted on by the senior itself $x_{2(2)}^*$ would be larger than either the senior's share insisted on by the parent $x_{2(p)}^*$ or the senior's share insisted on by the age-1 junior $x_{2(1)}^*$ (proofs shall not be shown). Again, the necessary and sufficient condition for $x_{2(p)}^* < x_{2(2)}^*$ is:

$$\frac{\psi'(E_{x(p)}^*) r_{12}}{\psi'(E_{x(1)}^*) r_{1p}} > r_p = 0.5. \quad (4.18)$$

For full-siblings, r_{12}/r_{1p} can be ignored and thus whether inequality 4.18 holds or not depends on the value of $\psi'(E_{x(p)}^*)/\psi'(E_{x(1)}^*)$, which will be slightly less than unity. Consequently, for full siblings, the senior's optimal resource from the parental perspective $x_{2(p)}^*$ will be less than the senior's share from the junior's perspective $x_{2(1)}^*$, unless the marginal cost of current total investment to the parental residual survival

declines too abruptly. By contrast, for a single parent looking after two half-siblings, it is always the junior sibling who insists on the least amount of resources for the share of the senior sibling.

Figure 4.4 shows the battleground of three-way family conflicts between a parent, its senior offspring, and junior offspring over the optimal allocation of parental resources, for the case of full-siblings. As to the senior sibling's 'fair' share, for example, all family members agree that the senior should receive parental resources to some extent (see fig 4.4a). However, unless the marginal cost of total investment to the parent's residual survival declines too rapidly, it is the parent who wants to allocate the least amount of resources for the senior sibling. Hence conflict ensues between the parent and its two siblings: in this zone of conflict, increasing the amount of resources for the senior sibling is advantageous to both siblings but harmful to the parent. A different form of family conflict is also possible, because it is the senior sibling itself who insists on the greatest amount of resources for the senior. In the zone of conflict between the senior sibling versus others (the parent and the junior sibling), increasing the resource level for the senior is advantageous to the senior but disadvantageous to both the parent and the junior sibling. Above the level of optimal PI from the senior's own perspective, no family member wants to increase the resource level and hence no conflict occurs (fig 4.4a). It is worth noting that, as the age spacing between two siblings increases, all family members insist that the ideal share of PI for the senior sibling should increase. Figure 4.4b illustrates the family conflict over the optimal PI for the junior sibling, which shows qualitatively the same pattern as Figure 4.4a. In general, among family members, it is the focal offspring itself who insists on the greatest amount of resources for the focal offspring. In most cases (especially for full-siblings), the parent insists on the least for the focal offspring and the focal offspring's sibling insists on the intermediate. Figure 4.4b also indicates that, as the age gap increases, the ideal shares for the junior sibling from each member's perspective all decrease.

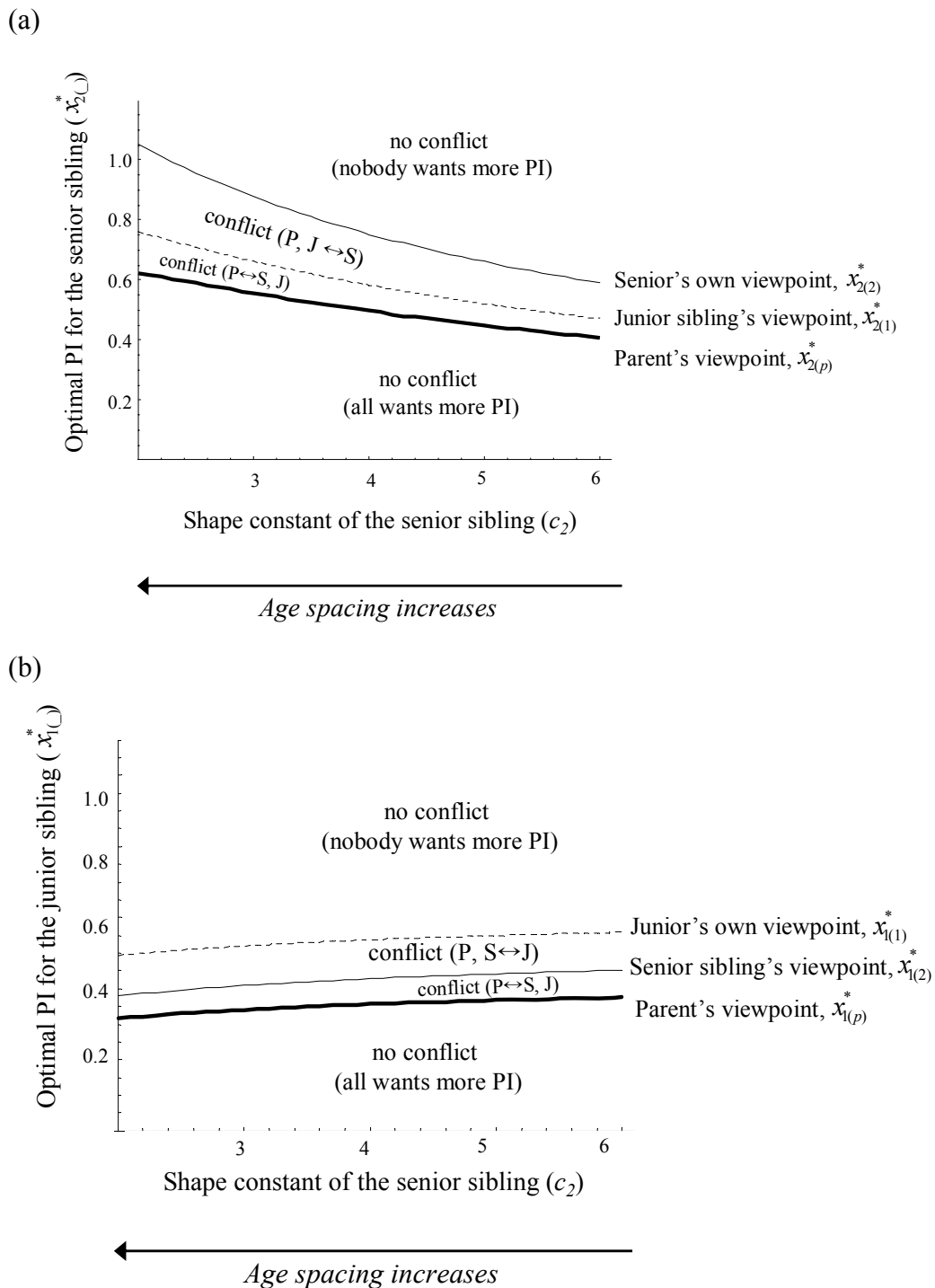


Figure 4.4. The battleground of three-way family conflicts between a parent, its senior offspring, and its junior offspring over the optimal allocation of parental resources. (a) the disagreement over the optimal amount of resources for

the senior sibling. (b) the disagreement over the optimal amount of resources for the junior sibling. Parameters used are the same as Figure 4.3.

Figure 4.5a shows the evolutionary conflicts over the total amount of PI that should be delivered for a current feeding episode. Unsurprisingly, the total amount of PI that serves the interests of either sibling is higher than the total PI serving the parental interests (fig 4.5a). As the senior sibling's age increases with the junior sibling's age being fixed, each family member insists that the total amount of PI should increase. In order to see how family members disagree about the division of PI among different-aged offspring as well as the total amount of PI to be delivered, the optimal resource bias toward the senior offspring, measured as $x_2^*/(x_1^* + x_2^*)$, was plotted for each family member's viewpoint (fig 4.5b). It is revealed that the optimal bias of PI toward the senior sibling is highest for the senior itself, followed by the parent, and the junior sibling. All family members agree that, the larger the age spacing between two siblings, the more resource the senior should get. Importantly, figure 4.5b shows that the disagreement over how to divide PI among two siblings remains relatively constant over the range of age spacing: the lines of optimal bias do not converge across the shape constant of the senior sibling. This indicates that the genetic potential for intrafamilial conflicts is maintained irrespective of the age spacing between siblings. Nevertheless, there may be an interesting implication resulting from the age spacing. When age gap is close, the junior offspring wants to get more than its senior sibling; however, when age gap is large, the junior offspring want to get less than its senior sibling (see fig 4.5b).

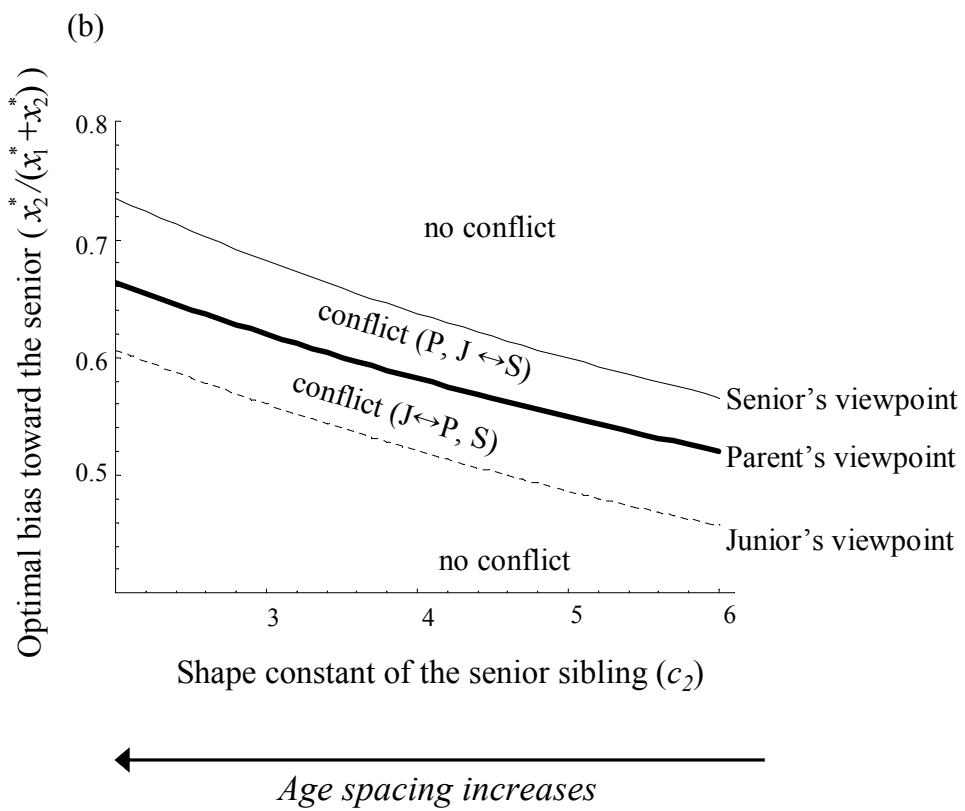
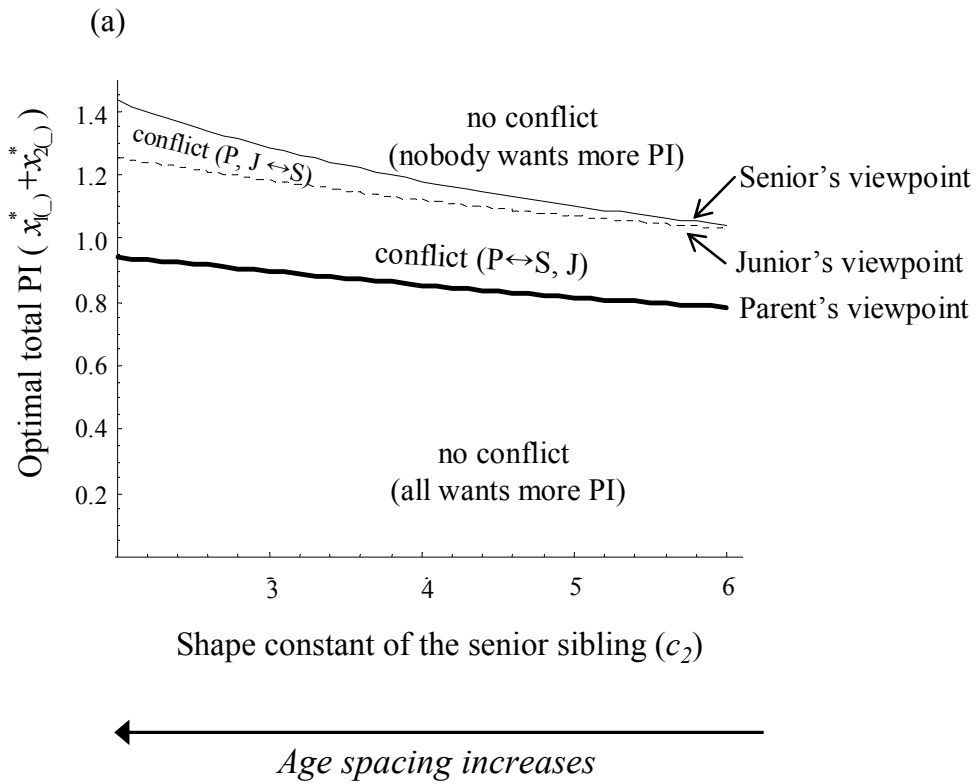


Figure 4.5. Evolutionary conflicts of interests over (a) the total amount of PI that should be delivered for a current feeding episode and (b) the optimal resource bias toward the senior sibling. The bias was measured as $x_2^*/(x_1^* + x_2^*)$. Note that the bias toward the senior from the perspective of the junior sibling is below 0.5 if the age spacing is close enough, i.e., the junior wants to get more resources in such situations. The bias toward the senior exceeds as the age spacing increases. The same parameters were used.

DISCUSSION

The results described above indicate that, if family members were allowed to differ in their ages, the classic picture of Trivers' (1974) parent-offspring conflict should be fundamentally revised. Taking into account the role of age-specific reproductive value, one can no longer expect that each individual offspring should favor a preferential investment of PI toward itself whereas parents should prefer an equal allocation of PI across all offspring. The results of this chapter are summarized as follows:

1. A senior sibling wants the parent to invest more in itself than in its younger sibling.
2. If age spacing is close enough, a junior sibling wants the parent to invest more in itself than in its senior. However, if the age spacing is large enough, a junior sibling wants the parent to invest *less* in itself than its senior.
3. In most situations composed of full siblings, each family member (a parent, its senior offspring, and junior offspring) will disagree over the optimal amount of resources for a focal offspring. The focal offspring insists on the largest amount of resources for itself, followed by its sibling, and by the parent the least.

4. As the age gap between siblings increases, all family members increasingly favor biased allocation of PI toward the senior sibling. Yet each family member continues to disagree over how strongly the senior sibling should be favored; hence the potential of intrafamilial conflict is maintained irrespective of age spacing.

Previous models of intrafamilial conflict have not explored how the optimal allocation of PI from the viewpoint of each individual offspring would be shaped according to the age composition of the brood. Indeed, the two counteracting effects of offspring growth on PI allocation – the elder sibling has a higher reproductive value and yet the junior sibling benefits more from a unit of extra resources – has hindered the full analysis of sibling competition over parental resources. For instance, Dawkins (1976, p. 128) argued that a senior sibling may at times favor biased allocation of foods toward its junior sibling because of the junior's higher needs for foods. By contrast, the formal model presented here demonstrates that a senior sibling will always want biased allocation toward itself despite (in fact, because of) its junior sibling's higher needs for foods. Equation (4.8), a marginal version of Hamilton's rule that correctly weighted each family member's fitness change by its age-specific reproductive value, produces those results if the junior sibling could benefit more from a unit of additional resources than the senior.

Contrary to Trivers' (1974) insight that each individual offspring should strive to get more resources for itself because each one is doubly related to itself, the current model reveals that a junior sibling will want less resources for itself than its senior sibling if the age spacing between them is sufficiently wide. The biased allocation in favor of senior siblings, a widespread phenomenon reported in almost all asynchronously hatching birds and mammals (Mock & Parker, 1997), hence does not necessarily imply that the junior siblings 'lose' the conflict with senior siblings or parents. Although a junior sibling may want less resources than its senior if the age

spacing is wide, this should not be taken to mean that the potential for genetic conflict between family members is diminished with the increment of age spacing. Rather, the potential for intrafamilial conflict is almost constantly maintained without regard to age spacing (see fig 4.5b). The reason is that the degree of favoring the senior from the perspective of either the senior itself or the parent continues to be higher than the degree of favoring the senior from the perspective of the junior.

Therefore, if we measure the potential for intrafamilial conflict as the magnitude of PI range over which the evolutionary interests of family members are in conflict (Godfray, 1995a; Trivers, 1974), it can be said that age differences between siblings has little influence on aggravating or reducing conflicts within the family. This may have a profound implication on the hypothesis that hatching asynchrony and its consequent age asymmetries among siblings may have evolved as parental adaptations to reduce sibling competition (Hahn, 1981; Mock & Ploger, 1987). Since the model presented here is a battleground model that identifies the different optima for a parent and its multiple offspring of differing ages, how age asymmetries among siblings affect the resolution of conflict should be explicitly modeled by future studies.

As it applies to the human family, the model presented here may provide a useful theoretical framework for analyzing sibling relationships in childhood and early adolescence. For instance, in a preliminary study college students were asked to divide an amount of hypothetical pocket money between themselves and their actual siblings. It was found that they allocated more money for themselves if their counterparts are their junior siblings. Yet they allocated less money for themselves if their counterparts are their senior siblings provided that the age spacing is wide enough (J. Jeon, unpublished results).

Moreover, it has been known that each child has its unique perception about the fairness of parental preferential treatment (Kowal & Kramer, 1997; Kowal, Kramer, Krull, & Crick, 2002; Kowal, Krull, & Kramer, 2004). The current model suggests that

a certain child's subjective criteria for judging whether parental resources are 'fairly' distributed among itself and its siblings may be a manifestation of specifically designed psychological mechanisms, whose function is to achieve the optimal allocation of PI from the focal child's perspective. Consequently, it would be interesting to investigate if specific patterns of PI allocation that are perceived as 'fair' by children are in good accord with the ideal allocation pattern of PI that must have maximized the children's inclusive fitness in ancestral environments, as predicted by the model developed here.

In summary, this study explored how intrafamilial conflicts over the allocation of parental resources take place between a parent, its senior offspring, and its junior offspring. If age spacing between siblings is close enough, each individual offspring favors preferential investment toward itself rather than its siblings. If age spacing is distant enough, however, the junior sibling agrees that the senior should get more resources from the parent. Yet the potential for family conflicts does not weaken, because the senior sibling favors far more biased allocation than the junior sibling allows. The results suggest that the classic picture of Trivers' (1974) parent-offspring conflict may be too simplistic and needs to be substantially revised.

SUPPLEMENTAL DATA

4.1. Reproductive values and stable age distribution

Assuming that λ remains at 1 due to the density-dependent regulation, the vector of individual reproductive values $\mathbf{v}^* = [v_1^*, \dots, v_n^*, v_p^*]$ in the resident population be determined up to a scalar constant from the recurrence equation $\mathbf{v}^* \mathbf{A}^* = \mathbf{v}^*$. Since the eigenvector \mathbf{v}^* can be scaled at will, I choose the reproductive value of parents v_p^* to equal 1. Then the reproductive value of each offspring class is:

$$v_i^* = \prod_{k=i}^n \varphi_k^* \quad (i = 1, \dots, n) \quad (4A.1)$$

Likewise, the vector of stable age distribution $\mathbf{u}^* = [u_1^*, \dots, u_n^*, u_p^*]$ can be determined up to a constant from the recurrence equation $\mathbf{u}^* \mathbf{A}^* = \mathbf{u}^*$. By choosing the relative number of parental class u_p^* to 1, I obtain the relative number of each offspring class:

$$u_i^* = f \prod_{k=1}^{i-1} \phi_k^* \quad (i = 2, \dots, n) \quad (5A.2)$$

and u_1 is defined as f .

4. 2. Dynamical stability

Let the vector of the inclusive fitness effects \mathbf{W}_{inc} of a focal offspring's deviant allocation be $[\Delta W_{x_1}, \Delta W_{x_2}, \dots, \Delta W_{x_n}]$. In order to check whether a focal offspring's equilibrium strategy $\mathbf{x}^* = [x_1^*, x_2^*, \dots, x_n^*]$ represents a set of attractors over evolutionary time, I employ the following evolutionary dynamic (Abrams, Matsuda, & Harada, 1993; Greenwood-Lee, Taylor, & Haig, 2001; Wild & Taylor, 2004):

$$\frac{d}{dt} \begin{bmatrix} x_1 \\ x_2 \\ \vdots \\ x_n \end{bmatrix} = \begin{bmatrix} \sigma_{x_1}^2 & \sigma_{x_1 x_2} & \dots & \sigma_{x_1 x_n} \\ \sigma_{x_2 x_1} & \sigma_{x_2}^2 & \dots & \sigma_{x_2 x_n} \\ \vdots & \vdots & \ddots & \vdots \\ \sigma_{x_n x_1} & \sigma_{x_n x_2} & \dots & \sigma_{x_n}^2 \end{bmatrix} \begin{bmatrix} \Delta W_{x_1} \\ \Delta W_{x_2} \\ \vdots \\ \Delta W_{x_n} \end{bmatrix}, \quad (4A.3)$$

where the constant $\sigma_{x_i}^2$ is the additive genetic variance of trait x_i , the constant $\sigma_{x_i x_j}$ ($i \neq j$) is the additive genetic covariance between x_i and x_j , and the notation d/dt is differentiation with respect to evolutionary time. Since the elements of the allocation vector were assumed to be genetically uncorrelated with each other, the off-diagonal elements of the covariance matrix in equation (5A.3) are all zero. For the equilibrium strategy \mathbf{x}^* to be a dynamically stable strategy (DSS), the Jacobian matrix

$$\mathbf{J} = \begin{bmatrix} \sigma_{x_1}^2 & 0 & \dots & 0 \\ 0 & \sigma_{x_2}^2 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \sigma_{x_n}^2 \end{bmatrix} \begin{bmatrix} \frac{\partial \Delta W_{x_1}}{\partial x_1} & \frac{\partial \Delta W_{x_1}}{\partial x_2} & \dots & \frac{\partial \Delta W_{x_1}}{\partial x_n} \\ \frac{\partial \Delta W_{x_2}}{\partial x_1} & \frac{\partial \Delta W_{x_2}}{\partial x_2} & \dots & \frac{\partial \Delta W_{x_2}}{\partial x_n} \\ \vdots & \vdots & \ddots & \vdots \\ \frac{\partial \Delta W_{x_n}}{\partial x_1} & \frac{\partial \Delta W_{x_n}}{\partial x_2} & \dots & \frac{\partial \Delta W_{x_n}}{\partial x_n} \end{bmatrix} \quad (4A.4)$$

should be negative definite at the equilibrium point $[x_1^*, x_2^*, \dots, x_n^*]$ (Wild & Taylor, 2004). In other words, $\mathbf{z}^T \mathbf{J} \mathbf{z}$ should be negative for all nonzero vectors \mathbf{z} when \mathbf{J} is evaluated at equilibrium. Recall that an age- i offspring survival $\varphi_i(x_i)$ increases with the amount of resources provided, with diminishing returns: $\partial^2 \varphi_i(x_i) / \partial x_i^2 < 0$. No genetic correlation was assumed among each different-aged offspring's resource share: $\partial^2 \varphi_i(x_i) / \partial x_i \partial x_j = 0$ ($i \neq j$). Moreover, the parent's residual survival is a decreasing, concave-down function of current total expenditure: $\partial^2 \psi(E_x) / \partial E_x^2 < 0$. Taking these into account, one can verify that $\mathbf{z}^T \mathbf{J} \mathbf{z}$ is negative for all nonzero vectors \mathbf{z} .

Chapter 5: Altruism towards cousins

SUMMARY

Recent research on kin investment shows a matrilineal bias as a function of paternity uncertainty. Kin investment, however, is a special case of kin altruism. It is thus hypothesized that psychological adaptations have evolved to regulate cousin-directed altruism according to predictably variable levels of paternity uncertainty in different categories of cousins. I develop a formal mathematical model that predicts that individuals should be most willing to act altruistically toward their mother's sister's children and least willing to act altruistically toward their father's brother's children. Altruism toward father's sister's and mother's brother's children are predicted to fall in between. An empirical study ($N = 195$), assessing expressed altruistic proclivities, confirmed predictions from the model. Participants expressed willingness-to-help following this descending order, 1) mother's sister's children, 2) mother's brother's children, 3) father's sister's children, and 4) father's brother's children. The psychological variables of emotional closeness, empathic concern, and contact frequency showed precisely the same pattern across distinct cousins, providing convergent confirmation of the model. The results support the hypothesis of cousin-specific adaptations sensitive to varying probabilities of paternity uncertainty.

INTRODUCTION

Kin relationships are composed of many subunits such as motherhood, fatherhood, grandparenthood, and sibship. Evolutionary approaches suggest that qualitatively distinct kin relationships have posed recurrently different adaptive problems to human ancestors, resulting in relationship-specific psychological adaptations (Kurland &

Gaulin, 2005; Wilson & Daly, 1997). The evolved psychologies of motherhood and fatherhood have been actively explored in recent decades (Geary, 2005; Salmon, 2005). The study of grandparents, uncles, and aunts has received some attention (Euler & Weitzel, 1996; Gaulin, McBurney, & Brakeman-Wartell, 1997; Michalski & Shackelford, 2005). Aside from the anthropological investigation of cousin marriages (Levi-Strauss, 1969), the psychology of cousin relationships has remained entirely unexplored.

Due to a key feature of mammalian, primate, and human reproductive biology—internal female fertilization—paternity probability has proven a key predictor of paternal investment. Since women may cuckold their long-term mates through extra-pair copulations, males experience reduced paternity. Not all of men's putative offspring are their genetic offspring. Because compromised paternity probability reduces the reproductive payoff of a male's investment, selection should favor reducing investment in response to reduced paternity (Houston & Davies, 1985; Trivers, 1972; Winkler, 1987). In humans, considerable empirical evidence indicates that fathers do invest less in parental care as their paternity is reduced (Anderson, Kaplan, & Lancaster, 1999; Marlowe, 1999).

Reduced paternity has also been shown to affect the investment strategies of grandparents. Because the vertical links through males are less certain than the links through females, the number of uncertain links between distant family members theoretically should predict interactions with distant kin. For example, a maternal grandmother is connected to her grandchildren through two certain links; a maternal grandfather and a paternal grandmother are connected through one certain and one uncertain link; and a paternal grandfather is connected through two uncertain links. Smith (1988) predicted that maternal grandmothers should invest in their grandchildren the most, followed by both maternal grandfathers and paternal grandmothers, with paternal grandfathers investing the least. Empirical tests supported the prediction

(DeKay, 1995; Euler & Weitzel, 1996; Laham, Gonsalkorale, & von Hippel, 2005; Michalski & Shackelford, 2005; Pashos, 2000). Matrilateral aunts and uncles are predicted to invest more in nieces and nephews than patrilateral aunts and uncles. The laterality and sex-of-investor biases have been documented (Gaulin et al., 1997; McBurney, Simon, Gaulin, & Geliebter, 2002).

Because investment in kin of the next generation constitutes just one form of kin altruism, the logic of differential altruism as a function of differential paternity uncertainty should extend to investment patterns among cousins. Cousins come in four categories based on relationship to the focal individual: mother's sister's (MoSis) children; mother's brother's (MoBro) children; father's sister's (FaSis) children; and father's brother's (FaBro) children. A focal individual can be completely "certain" (no conscious awareness implied) that all putative MoSis children are genetically related to herself or himself by a coefficient of relatedness of one-eighth. One uncertainty link occurs for putative FaSis children and MoBro children. And two uncertainty links occur for putative FaBro children (see Figure 5.1) (although there could be another uncertain genetic link between the focal individual's parent and her or his aunts/uncles, such uncertainty would be the same across each cousin categories and hence can be ignored for the present purposes). I therefore hypothesized that psychological adaptations have evolved to regulate cousin-directed altruism in response to the varied levels of paternity uncertainty across categories of cousins. I construct a kin selection model of altruism toward distinct cousins, showing that hypothesized evolved decision rules will lead one to act most altruistically toward one's MoSis children, followed by both FaSis children and MoBro children, and lastly FaBro children (see Supplemental data 5.1).

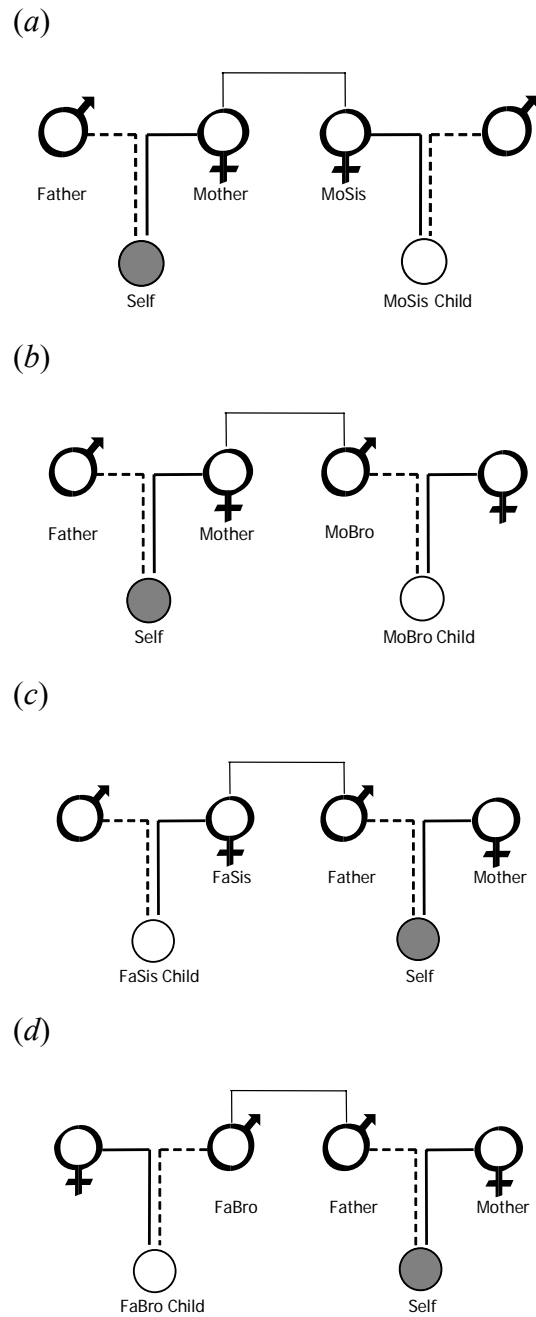


Figure 5.1. The genealogical links between self and different categories of cousins. (a) A self and its mother's sister's (MoSis) children. (b) A self and its mother's brother's (MoBro) children. (c) A self and its father's sister's (FaSis) children. (d) A self and its father's brother's (FaBro) children. The dashed line (---) indicates that within-pair paternity might be reduced due to cuckoldry.

Based on this formal model of discriminative cousin altruism, this chapter presents empirical tests of the model's key prediction that willingness to act altruistically toward cousins will follow the order (1) MoSis children, (2) both MoBro and FaSis children, and (3) FaBro children. I conducted a study that explored willingness to help cousins using hypothetical dilemmas involving life-and-death situations. Recent research has shown that psychological variables such as emotional closeness, empathic concern, and the frequency of contact may mediate the effect of genetic relatedness on decisions to act altruistically toward kin (Korchmaros & Kenny, 2001, 2006; Neyer & Lang, 2003). I predicted that emotional closeness, empathic concern, and frequency of contact would also follow the same order across the distinct categories of cousins, affording three additional empirical tests of the model.

METHOD

Participants

One hundred ninety-five undergraduate students from the University of Texas at Austin (84 women and 111 men) participated in this study. It was made clear in the recruiting stage that only those with one or more cousins would be eligible to participate. The mean age of participants was 19.8 (\pm S.D. 1.5) years (range=18–27).

Investment Instrument

The first section of the instrument requested basic demographic information of participants (age, sex, ethnicity, and socioeconomic status (SES)). I explicitly defined the four categories of cousins so that participants could clearly distinguish each cousin category (e.g., "paternal aunt's children (=father's sister's children)"). Participants were asked to consider only their "blood-related" cousins and to ignore any genetically unrelated cousins through stepparents or foster parents. For each cousin category,

participants were instructed to think of the cousin whose age is closest to their own. This restriction was designed to prevent introducing any bias that might occur if participants chose their favorite cousin from each type of cousin. The demographic information (age, sex, and SES) of each cousin was obtained. The remaining sections of the instrument were repeated for each category of cousins; hence, participants who had all four categories of cousins answered four times for each question.

The second section assessed psychological variables hypothesized to mediate the association between genetic relatedness and kin-directed altruism: emotional closeness, empathic concern, and the frequency of contact. Participants evaluated, using a seven-point rating scale from 1 (not at all) to 7 (very much), how emotionally close they felt to each cousin. Using the same seven-point scale, they also evaluated how much they cared for the well-being of each cousin. They further evaluated, on a ten-point rating scale from 1 (never) to 10 (every day), how often they communicated with each person by email, phone, letter, or in person.

The third section measured participants' willingness to act altruistically toward cousins in a hypothetical dilemma involving life-or-death situations. Participants read the following scenario:

As you make your way through the city you walk past a building that is blazing with flames. You instantly realize that the building has been housing a meeting attended by your cousin _____ (fill in the initials). Your cousin _____ in the rapidly burning building badly needs your help, yet entering the burning building to save him or her would risk injury to you.

Participants were asked on a seven-point rating scale from 1 (extremely unlikely) to 7 (extremely likely): "How likely would you enter the burning building and attempt to save your cousin's life, despite the considerable harm to you?" Information about the

residential distances between participants and each category of cousins was collected in order to examine whether residential distance acts as a confounding variable that could affect the willingness-to-help scores. The rating scale was based on the logarithmic ten-point scale developed by Euler and Weitzel (1996).

Finally, I asked forced-choice questions about emotional closeness, empathic concern, and the willingness to help cousins. Participants were asked, for example, “Among those different kinds of cousins you actually have, which kind of cousin are you emotionally closest to?” Participants having only one category of cousin were instructed not to answer.

Data set and Statistical Analysis

Fifty six participants had all four categories of cousins. Statistical analyses were performed for those 56 participants having all four categories of cousins, and for all participants ($N = 195$) having at least one category of cousin. The number of cousin categories participants had did not affect the average rating of the willingness-to-help (one-way ANOVA, $F(3,194) = 1.24$, n.s.). Although the willingness-to-help scores and other psychological variables were negatively skewed (skewness coefficient = -1.00), parametric statistics were used in this study because the F statistic is quite robust to moderate violations of the normality assumption (Cohen, 1969). I confirmed that both non-parametric tests and data transformation to handle non-normality produce nearly identical results.

RESULTS

There were no significant main effects or interactions for sex of participant in responses on force-choice items or rating-scale items, nor were there any significant main effects or interactions for the sex of participants' cousins. Therefore, the data were

collapsed across the two variables (sex of participants, sex of participants' cousins) in subsequent analyses.

Forced-choice life-or-death data

The 56 participants who had all four categories of cousins were asked which cousin they would help the most in a hypothetical life-or-death situation. The overall null hypothesis would dictate that each category of cousins would be equally chosen by chance alone. The observed distribution of choices was 26:3:14:13 for mother's sisters' (MoSis) children, mother's brother's (MoBro) children, father's sister's (FaSis) children, and father's brother's (FaBro) children, respectively. A chi-square test revealed that the observed distribution was significantly different from the distribution expected by chance, supporting the first prediction in this study ($\chi^2 = 19.0$; $df = 3$; $p < .001$). Next, I collapsed the MoBro children and FaSis children into a single composite and tested the null sub-hypothesis of 1:2 for the MoSis children and the composite. A significant difference was also detected ($\chi^2 = 14.24$; $df = 1$; $p < .001$). Lastly, I tested the null hypothesis of 2:1 for the composite variable above and the FaBro children. The chi-square test failed to detect a significant difference ($\chi^2 = 1.35$; $df = 1$; $p = .245$). Therefore, the hypothesis that the order of willingness-to-help scores would be MoSis > MoBro = FaSis > FaBro was generally supported, except that FaBro children would be helped the least (Table 5.1).

Similar results were obtained for the forced-choice items about emotional closeness and empathic concern. For both items, the overall null hypothesis that each category of cousins would equally chosen was rejected. Further, the null subhypothesis of 1:2 for MoBro children and the composite variable noted above was rejected. The null subhypothesis of 2:1 for the composite variable and FaBro children, however, was not rejected (Table 5.1).

Table 5.1. Forced-choice data of willingness-to-help scores and other psychological variables for the subsample having all four cousin categories (n =56). (An asterisk (*) indicates significant differences ($p < .001$))

	Willingness -to-help	Emotional Closeness	Empathic concern
Observed distribution (MoSis: MoBro: FaSis: FaBro)	26:3:14:13	27:10:8:11	31:6:7:12
χ^2 of overall null hypothesis (MoSis: MoBro: FaSis: FaBro = 1:1:1:1)	19.0*	16.43*	29.0*
χ^2 of null hypothesis #1 (MoSis: MoBro + FaSis = 1:2)	14.24*	6.145*	27.28*
χ^2 of null hypothesis #2 (MoBro + FaSis: FaBro = 2:1)	1.35	0.277	2.42

Willingness to act altruistically, emotional closeness, empathic concern, and frequency of contact

Willingness to act altruistically toward cousins

The prediction was that willingness to act altruistically toward cousins would be arranged in the following order: (1) MoSis children, (2) both MoBro and FaSis children, and (3) FaBro children. I controlled for the effects of the residential distance between participants and each of their cousins and the age difference between the two. Cousins who happened to live close to each other would have more opportunities to develop cooperative relationships than those living far away, so the residential distance may act as a confound. Indeed, for the total sample of participants, repeated measures ANOVA revealed that the residential distance between participants and cousins was marginally significantly different across the four cousin categories ($F(3, 355) = 2.558, p = .055$). Another potential confound is age, since the age differences between participants and

their cousins may affect cousin-directed altruism. For the total sample, the age difference between participants and cousins differed significantly across the four cousin categories ($F(3,355) = 5.952, p = .001$). Thus, subsequent analysis included the residential distance and the age difference as covariates.

Repeated measures analysis of covariance (ANCOVA) with the two covariates was conducted on the willingness-to-help scores for the total sample of participants. There was a highly significant main effect of different cousin categories on the willingness-to-help scores ($F(3,352) = 10.848, p < .001$). The mean ratings were arranged in the following order: MoSis children, MoBro children, FaSis children, and FaBro children (Table 5.2). A significant linear trend was revealed ($F(1,352) = 28.489, p < .001$). The results confirm the first prediction that cousin-directed helping tendencies would be arranged in the order of (1) MoSis children, (2) both MoBro and FaSis children, and (3) FaBro children. Planned repeated comparisons where adjacent group means are compared showed that participants were significantly more willing to help their MoSis children than their MoBro children ($p = .001$), but not significantly more willing to help their MoBro children than their FaSis children ($p = .616$). Participants were slightly more willing to help their FaSis children than their FaBro children, although this comparison did not reach statistical significance ($p = .151$). Overall, the difference between the adjusted means of FaSis children and FaBro children was much greater than the difference between MoBro children and FaSis children (Fig. 5.2).

Table 5.2. Raw and (adjusted) mean ratings of willingness-to-help across distinct cousin categories, adjusted for age differences and residential distance.

category of cousins	total sample (<i>n</i> = 195)			those having all four cousins (<i>n</i> = 56)	
	Mean	S.D.	N	Mean	S.D.
MoSis children	6.05 (6.12)	1.42	149	5.89 (5.88)	1.23
MoBro children	5.73 (5.74)	1.46	148	5.59 (5.58)	1.36
FaSis children	5.59 (5.68)	1.32	126	5.39 (5.42)	1.55
FaBro children	5.50 (5.51)	1.11	131	5.34 (5.34)	1.67

A similar analysis for the subset of participants having all four categories found the same pattern. The effect of the different cousin categories on the willingness-to-help scores was significant (repeated measures ANCOVA, $F(3,163) = 3.813, p = .011$), and a significant linear trend was detected ($F(1, 163) = 10.60, p = .001$). Due to the reduced sample size, planned repeated comparisons revealed that only the difference between the adjusted ratings of MoSis children and MoBro children was marginally significant ($p = .084$). Given that both samples show the same pattern of ratings, I hereafter focus on the total sample, which had greater statistical power.

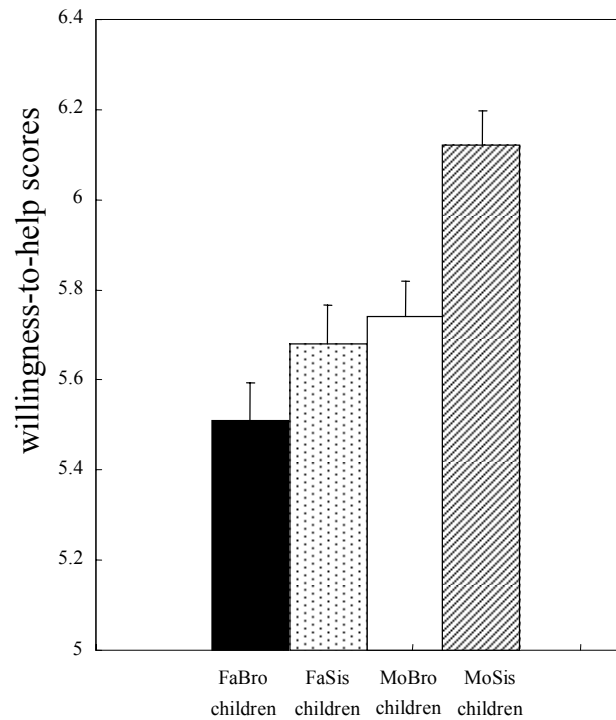


Figure 5.2. The adjusted mean ratings (and standard error) of willingness-to-help scores among four different cousin categories, controlling for age differences and residential distance.

Emotional closeness, empathic concern, and the frequency of contact

The ratings of three possible predictors of cousin-directed altruism were significantly correlated with one another ($r = .59$ for emotional closeness and concern, $r = .72$ for emotional closeness and contact, and $r = .45$ for concern and contact: all $ps < .01$). These correlations provide circumstantial evidence for the reliability and validity of these variables as indices of altruism toward cousins. Indeed, each of the predictors was significantly correlated with the willingness-to-help scores ($r = .44$ for empathic concern, $r = .42$ for emotional closeness, and $r = .31$ for contact frequency: all $ps < .01$).

To test the prediction that the three predictors should also be arranged in the order predicted by the formal model, a repeated measures ANCOVA including residential

distance and age differences as covariates was conducted on each variable. Emotional closeness ratings were significantly different across distinct cousin categories ($F(3,352) = 10.961, p < .001$), showing a significant linear trend ($F(1,352) = 28.13, p < .001$) in which the adjusted mean ratings were arranged in the same way as willingness-to-help ratings (Table 5.3). Planned repeated comparisons found that the difference between MoSis children and MoBro children was significant ($p = .001$). Neither the difference between MoBro children and FaSis children nor between FaSis children and FaBro children was significant.

Analyses conducted on empathic concern ratings revealed a significant main effect of different cousin categories on empathic concern (repeated measures ANCOVA, $F(3,352) = 5.548, p = .001$), revealing a significant linear trend ($F(1,352) = 10.367, p = .001$). Consistent with the prediction, the adjusted mean ratings were arranged in the descending order of (1) MoSis children, (2) FaSis Children, (3) MoBro children, and (4) FaBro children.

The ratings of contact frequency were also significantly different among different cousin categories (repeated measures ANCOVA, $F(3,352) = 8.492, p < .001$) and showed a significant linear trend ($F(1,352) = 19.99, p = .001$). The adjusted mean ratings were arranged in the same way as empathic concern. Participants concerned about their MoSis children significantly more than their FaSis children ($p < .001$), not significantly concerned their FaSis children than their MoBro children ($p = .851$), and not significantly concerned their MoBro children than their FaBro children ($p = .174$).

Table 5.3. Raw and (adjusted) mean ratings of emotional closeness, empathic concern, and contact frequency across distinct cousin categories for the total samples of participants, adjusted for age differences and residential distance.

category of cousins	N	emotional closeness		empathic concern		contact frequency	
		Mean	S.D.	Mean	S.D.	Mean	S.D.
MoSis children	149	4.70(4.56)	1.61	5.69(6.04)	1.47	5.25(5.13)	2.35
MoBro children	148	3.91(3.88)	1.65	6.02(5.58)	1.22	4.33(4.28)	2.24
FaSis children	126	3.57(3.58)	1.96	5.53(5.61)	1.54	4.16(4.32)	2.17
FaBro children	131	3.66(3.49)	1.90	5.51(5.53)	1.57	4.00(3.97)	1.99

DISCUSSION

The current research investigated the hypothesis, derived from a formal mathematical model, that humans have relationship-specific psychological adaptations for cousin-directed altruism sensitive to the different levels of paternity uncertainty across categories of cousins. Based on the varied paternity probability, the model of altruism toward cousins predicted that MoSis children would be the most favored, followed by both MoBro and FaSis children, with FaBro children coming out last. Participants reported a willingness to act altruistically toward their MoSis children the most, followed by their MoBro children, their FaSis children, and lastly their FaBro children. These results strongly confirm the central prediction from the model. Moreover, the pattern of psychological predictors of kin-directed altruism – emotional closeness, empathic concern, and contact frequency – across distinct cousin categories provided three additional confirmations of the model's predictions.

The present study failed to detect a statistically significant difference between ratings of altruism toward FaSis children and toward FaBro children. It is reasonable to conclude, however, that FaSis children are the least likely to be helped among all four cousin categories, because (1) the mean rating of FaSis children was invariably the lowest in the willingness-to-help scores as well as in all three psychological variables affecting altruism; (2) the predicted linear trends proved to be highly significant for all four dependent measures; and (3) FaSis children were helped more than FaBro children, as predicted, although it just missed conventional significance. Given that MoSis children were always ranked at the top position with a high statistical significance ($p \leq .001$) for all dependent measures, it remains to be revealed why the degree to which FaBro children are the least likely to be helped appears not to be as robust as expected.

Previous studies on the effect of paternity uncertainty on kin relationships have centered on investment in putative kin of the next generations, notably paternal investment, grandparental investment, and the investment of aunts and uncles (Geary, 2005; Kurland & Gaulin, 2005). To my knowledge, the present research is the first study to show that *differential altruism toward kin of the same generation* also can be predicted by varying levels of paternity probability. Whereas people apparently have the intuitive notion that reduced paternity results in reduced investment into the next-generation kin (e.g., as reflected in the folk saying “Mama’s baby, Papa’s maybe”) (Buss, 2000), it remains to be clarified at the proximate level the precise mechanisms by which altruism toward different cousins is affected by variable levels of paternity uncertainty in the parental generation.

One hypothesis is that altruistic tendencies toward their cousins will be largely determined by the quality of adult sibling relationship linking two families in the parental generation (J. Woolley, 2006, personal communication). Contact and affection between siblings in adulthood appears to be greater in sister-sister pairs than in mixed-sex pairs, with brother-brother pairs having the least contact and affection (White & Riedmann, 1992). Thus, an individual may be willing to help the MoSis children the most because mothers have kept on good terms with each other as sister-sister dyads. The hypothesis is consistent with the previous findings (1) that matrilineal aunts and uncles invest more in their nephews and nieces than patrilineal aunts and uncles, and (2) that aunts invest more than uncles regardless of laterality (Gaulin et al., 1997; McBurney et al., 2002). Indeed, the sister-sister adult dyads are most likely to invest in each other’s children (i.e., in their nephews and nieces) due to the absence of reduced maternity from each sister’s viewpoint, thus maintaining more cooperative relationships than other types of adult sibling dyads. This could represent one proximate path through which the predicted

discriminative altruism toward cousins occurs. In short, evolved decision rules for cousin-directed altruism may have been designed to convert important environmental inputs, such as the quality of sibling relationships in the parental generation, into the cognitive or behavioral outputs for discriminative altruism toward cousins.

Other environmental inputs processed by psychological adaptations for cousin-directed altruism may include the age differences between cousins and the amount of contact early in life resulting from residential distance (the two variables that were treated as covariates in this study). The age differences and residential distance may reflect sex differences in age at marriage and dispersal, respectively (Euler & Weitzel, 1996; Gaulin et al., 1997). Because men on average marry later in life than women do, it follows that 1) FaSis children will be older on average than one's own siblings; 2) MoBro children will be younger on average than one's own siblings; and 3) FaBro and MoSis children will be the same age on average. The mean age differences across distinct cousin categories in the current study were (-1.34):(+1.18):(-1.87):(+0.37) for FaBro children: FaSis children: MoBro children: MoSis children, respectively, which roughly coincides with my inference. Because individuals should be more willing to help their cousins younger than themselves and less willing to help cousins older than themselves, altruism toward MoBro children may be augmented and altruism toward FaSis children reduced due to the age differences between a focal individual and each category of his or her cousins.

The current research is based on the assumption that the information gained from self-reports reliably reflects the actual altruistic behavior toward kin. Previous studies of kin investment have shown that it does correspond well to the actual altruistic behavior. Sears, Mace, and McGregor (2000) found that Gambian children with a living maternal grandmother have better chances of survival than other children (Kurland & Gaulin,

2005). Further, there exist no known methodological biases that would have caused the participants to report their altruistic tendencies, emotional closeness, empathic concern, and contact frequency in ways that all correspond precisely with the *a priori* theoretical predictions.

In conclusion, the current results support the hypothesis that humans have evolved psychological adaptations regulating discriminative altruism toward cousins that are sensitive to varying numbers of paternity uncertainty links that characterize the distinct cousin categories. The current research is important because it shows that the laterality bias resulting from paternity uncertainty exists not only in investment in kin of the next generations, as others have demonstrated, but also in kin altruism toward the same generation, which this study is the first to demonstrate. The current study reveals an important theoretically-predicted design feature of cousin relationships, and consequently contributes to a growing body of literature of kinship adaptations.

SUPPLEMENTAL DATA

5.1. The Model of Cousin Altruism

I explore how a focal individual's altruistic effort toward each category of cousins is related to the varied levels of paternity in the parental generation, based on Houston's (1995) framework of optimal paternal effort. Let x be the level of effort a focal individual invest in an altruistic act toward a certain recipient (who is the actor's cousin). I assume that $0 \leq x \leq 1$. I denote $F(x)$ as the recipient's reproductive success due to the altruistic act and $G(x)$ as the reproductive success of the actor from investing into cousins other than the recipient or not investing at all. Clearly, $F(x)$ will be an increasing function of x and $G(x)$ will be a decreasing function of x . The focal actor's inclusive fitness W by investing into a certain putative cousin can be written as follows:

$$W(x) = \frac{\rho}{8} F(x) + G(x), \quad (5A.1)$$

where the recipient's fitness change is weighted by the genetic relatedness between cousins, $\frac{1}{8}$, and ρ is the probability that the recipient is the actor's genetically related cousin. Note that, if the focal actor were to have only one category of cousins, $G(x)$ could be written as $\rho G_0(x)$. In that case, it is clear that the optimal effort x^* into a putative cousin does not depend on ρ . Since it is impossible that our ancestors have had only one category of cousins throughout evolutionary history, this possibility can be safely ignored.

A necessary condition for the optimal effort x^* is found by differentiating equation (5A.1) with respect to x :

$$\frac{\rho}{8} F'(x^*) + G'(x^*) = 0, \quad (5A.2)$$

where prime denotes differentiation with respect to x . The following second-order condition should also be satisfied in order for $W(x)$ to have a maximum at x^* :

$$\frac{\rho}{8} F''(x^*) + G''(x^*) < 0 \quad (5A.3)$$

Differentiating implicitly equation (5A.2) with respect to ρ , one can figure out how x^* changes with ρ :

$$\frac{dx^*}{d\rho} = -\frac{F'(x^*)}{\rho F''(x^*) + 8G''(x^*)}. \quad (5A.4)$$

Reflecting equation (5A.3), it is obvious that the optimal effort x^* is positively related to ρ , the probability that one's putative cousin is indeed one's genetically related cousin. Denoting P as the population-average within-pair paternity, one can see that ρ s for MoSis children, MoBro children, FaSis children, and FaBro children are 1: P : P^2 , respectively (see Fig. 5.1). Since reduced ρ results in reduced optimal effort x^* into altruism toward cousins, the optimal efforts x^* toward distinct cousin categories are

$$x^*_{MoSis} > x^*_{MoBro} = x^*_{FaSis} > x^*_{FaBro}.$$

Chapter 6: Conclusion

Given that Hamilton's (1964) inclusive fitness theory provides an organizing theoretical framework for family relationships, why is it that evolutionary psychologists often have difficulty in making concrete predictions about kinship psychology? For instance, Daly and Wilson (1995) stressed that parents should favor offspring who are likely to yield a higher reproductive return on their parents' investment. Regarding birth order, then, which offspring should be favored by parents? As another example, does Hamilton's (1964) rule dictate that each child will necessarily want more resources for itself than its brothers and sisters, due to the logic of genetic relatedness?

These important questions about family dynamics could be answered by formally taking into account the role of reproductive value, Fisher's (1930) measure that makes it possible to compare the reproductive success of various individuals who may be in different states (e.g., age). This dissertation attempted 1) to construct evolutionary models of familial interactions based on reproductive value approach and 2) to characterize the design features of evolved kinship psychological mechanisms by empirically testing *a priori* predictions. In achieving these goals, a number of interesting results were gained. In this final chapter I briefly summarize my theoretical and empirical findings and suggest future areas of research.

OVERVIEW OF THE FINDINGS

Chapter 2 examined how parents are expected to allocate their parental investment among offspring of differing ages. Verbal reasoning of parental favoritism among offspring seemed almost impossible, because older offspring may be favored in terms of their higher reproductive value and yet younger offspring may be favored in terms of

their higher marginal return from additional resources. It was found that a parent's optimal strategy is to allocate his or her resources such that the marginal benefit to each offspring's survival, weighted by their survival probabilities to the reproductive age, should be equal to the marginal cost to the parent's residual survival. In nearly all circumstances, the parental optimum strategy will be realized as biasing parental resources toward older offspring.

The formal model developed in chapter 2 made different predictions from previous evolutionary hypotheses of human parental favoritism. Chapter 3 conducted an empirical study to evaluate these hypotheses, by asking human parents to hypothetically allocate tangible resources like food and money. Participants allocated more resources to the older children than the younger children, confirming the predictions obtained from chapter 2. A tentative scheme for the functional organization of psychological adaptations for allocating parental resources among different children was suggested.

Chapter 4 theoretically explored how each offspring will be selected to divide parental resources among itself and its siblings so as to maximize its own inclusive fitness. With the previous insights into the optimal allocation from the viewpoint of parents, chapter 4 also investigated how evolutionary conflicts of interests between family members of differing ages would take place. The model produced a number of interesting predictions on conflicts within the family. For example, it was predicted that a junior sibling may want less investment into itself than its senior sibling provided that the age spacing is sufficiently wide. Therefore, under wide age spacing between two siblings, sibling competition will revolve around how strongly the senior sibling should be favored, but not who should be favored.

Shifting the focus from close kin to distant kin such as cousins, chapter 5 tried to elucidate relationship-specific psychological adaptations specifically designed to regulate

discriminative altruism toward cousins. The empirical results showed that the laterality bias resulting from paternity uncertainty does exist not only in kin investment into the next generations, but also in kin altruism toward the same generation.

AVENUES FOR FUTURE RESEARCH

There are several areas that I plan to investigate based on the theoretical and empirical results obtained from this dissertation. First, future research should address how offspring qualities other than age (e.g., offspring sex or physical condition) would influence parental decision rules to divide limited resources among offspring. In other words, the architecture of parental psychological mechanisms for allocating resources among children should be documented at a comprehensive level. The problem of sex allocation, that is, how parents should divide resources between male and female offspring, has been extensively studied by evolutionary biologists (Charnov, 1982; Fisher, 1930; Frank, 1998; Hardy, 2002). Yet how parental resource allocation would be influenced by both offspring sex and age remains to be explored.

Second, chapter 4's predictions on sibling competition over parental resources should be empirically tested with human children. Some predictions that could be readily tested include: 1) as the age spacing increases, the senior sibling will want disproportionately more resources for itself than in its younger sibling and 2) as the age spacing increases, the junior sibling will want disproportionately *less* resources for itself than in its senior sibling. The predictions may be tested by asking children how they would like to allocate hypothetical or real resources among them and their counterpart siblings.

Third, the functional organization of cousin-directed altruism modules should be clearly identified. It is not easy to answer how differential altruistic tendencies toward

distinct categories of cousins are regulated by variable levels of paternity uncertainty in the parental generation. Chapter 5 suggested the quality of parental sibling relationship as an important environmental input that is processed by cousin-directed altruism mechanisms. More research is necessary, however, to fill in the gaps in our knowledge of how cousin-specific psychological adaptations develops and reliably operates throughout lifetime.

As a concluding remark, the studies presented here demonstrate that the evolutionary perspective has a great potential to revolutionize the study of human kinship in the near future. All too often, evolutionary perspective applied to human kinship is mistaken as something that exclusively focuses on the effect of genetic relatedness on family relationships. The theoretical framework provided here reveals that a wide variety of intrafamilial conflict is expected to take place even when all family members are identically related to each other by 0.5. Supplying a number of testable predictions about familial interactions and reporting noble empirical results on human kinship, the studies presented here could open a fruitful avenue for inferring the adaptive design of evolved psychological mechanisms for human kinship.

References

- Abrams, P. A., Matsuda, H., & Harada, Y. (1993). Evolutionary unstable fitness maxima and stable fitness minima of continuous traits. *Evolutionary Ecology*, 7, 465-487.
- Alexander, R. D. (1974). The Evolution of Social Behavior. *Annual Review of Ecology and Systematics*, 5, 325-383.
- Alexander, R. D. (1979). *Darwinism and human affairs*. Seattle: University of Washington Press.
- Anderson, K. G., Kaplan, H., & Lancaster, J. (1999). Paternal care by genetic fathers and stepfathers. II. Reports from Albuquerque man. *Evolution and Human Behavior*, 20, 405-431.
- Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation. *Science*, 211, 390-1396.
- Bjorklund, D. F., & Pellegrini, A. D. (2002). *The origins of human nature : Evolutionary developmental psychology*. Washington, DC: American Psychological Association.
- Bjorklund, D. F., & Yunger, J. (2001). Evolutionary Developmental Psychology: A Useful Framework for Evaluating the Evolution of Parenting. *Parenting*, 1, 63-66.
- Bogin, B. (1997). Evolutionary hypotheses for human childhood. *Yearbook of Physical Anthropology*, 40, 63-89.
- Borgerhoff Mulder, M. (1998). Brothers and sisters: how sibling interactions affect optimal parental allocations. *Human Nature*, 9, 119-162.
- Brody, G., Stoneman, Z., & Burke, M. (1987). child temperaments, maternal differential behavior, and sibling relationships. *Developmental Psychology*, 23, 354-362.
- Buss, D. M. (2000). *The dangerous passion: Why jealousy is necessary as love and sex*. New York: The Free Press.
- Buss, D. M. (2004). *Evolutionary psychology : the new science of the mind* (2nd ed.). Boston: Allyn and Bacon.
- Charlesworth, B. (1994). *Evolution in age-structured populations* (2nd ed.). Cambridge England ; New York: Cambridge University Press.
- Charnov, E. L. (1982). *The theory of sex allocation*. Princeton, NJ: Princeton University Press.
- Charnov, E. L. (1993). *Life History Invariants: Some explorations of symmetry in evolutionary ecology*. Oxford: Oxford University Press.
- Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton, NJ: Princeton University Press.

- Cohen, J. (1969). *Statistical power analysis for the behavioral sciences*. New York: Academic Press.
- Cosmides, L., & Tooby, J. (1992). Cognitive adaptations for social exchange. In J. H. Barkow, L. Cosmides & J. Tooby (Eds.), *The adapted mind* (pp. 163-228). New York: Oxford University Press.
- Cotton, P. A., Wright, J., & Kacelnik, A. (1999). Chick begging strategies in relation to brood hierarchies and hatching asynchrony. *American Naturalist*, *153*, 412-420.
- Daly, M., Salmon, C., & Wilson, M. (1997). Kinship: the conceptual hole in psychological studies of social cognition and close relationships. In D. T. Kenrick (Ed.), *Evolutionary social psychology* (pp. 265-296). Mahwah, N.J.: Lawrence Erlbaum Associates.
- Daly, M., & Wilson, M. (1988a). The Darwinian psychology of discriminative parental solicitude. *Nebraska Symposium on Motivation*, *35*, 91-144.
- Daly, M., & Wilson, M. (1988b). *Homicide*. New York: Aldine de Gruyter.
- Daly, M., & Wilson, M. (1995). Discriminative parental solicitude and the relevance of evolutionary models to the analysis of motivational systems. In M. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 1269-1286). Cambridge, MA: MIT Press.
- Davies, G. (2002). *A history of money from ancient times to the present day* (3rd edition ed.): University of Wales Press.
- Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.
- Day, T., & Taylor, P. D. (2003). Evolutionary dynamics and stability in discrete and continuous games. *Evolutionary Ecology Research*, *5*, 605-613.
- DeKay, W. T. (1995). *Grandparental investment and the uncertainty of kinship*. Paper presented at the 7th annual meeting of the Human Behavior and Evolution Society, Santa Barbara, CA.
- Dettwyler, K. A. (1995). A time to wean: the hominid blueprint for the natural age of weaning in modern human populations. In P. Stuart-Macadam & K. A. Dettwyler (Eds.), *Breastfeeding: Biocultural Perspectives* (pp. 39-73). New York: Aldine de Gruyter.
- Dunn, J., Stocker, C. M., & Plomin, R. (1990). Non-shared experiences within the family: correlates of behavior problems in middle childhood. *Development and Psychopathology*, *2*, 113-126.
- Eshel, I. (1983). Evolutionary and continuous stability. *Journal of Theoretical Biology*, *103*, 99-111.
- Eshel, I., & Motro, U. (1981). Kin selection and strong evolutionary stability of mutual help. *Theoretical Population Biology*, *19*, 420-433.
- Euler, H. A., & Weitzel, B. (1996). Discriminative grandparental solicitude as reproductive strategy. *Human Nature*, *7*, 39-59.

- Fisher, R. A. (1930). *The Genetical theory of natural selection*. Oxford: Oxford University Press.
- Frank, S. A. (1998). *Foundations of social evolution*. Princeton, N.J.: Princeton University Press.
- Frank, S. A. (2006). Social selection. In C. W. Fox & J. B. Wolf (Eds.), *Evolutionary genetics: concepts and case studies* (pp. 350-363). Oxford: Oxford University Press.
- Gaulin, S. J. C., McBurney, D. H., & Brakeman-Wartell, S. L. (1997). Matrilateral biases in the investment of aunts and uncles: a consequence of measure of paternity uncertainty. *Human Nature*, 8, 139-151.
- Geary, D. C. (2005). Evolution of paternal investment. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 483-505). Hoboken, N. J.: John Wiley & Sons.
- Geary, D. C., & Flinn, M. V. (2001). Evolution of human parental behavior and the human family. *Parenting*, 1, 5-61.
- Glasse, B., & Forbes, S. (2002). Begging and asymmetric nestling competition. In J. Wright & M. L. Leonard (Eds.), *The evolution of begging: competition, cooperation and competition*. Dordrecht, The Netherlands.: Kluwer Academic Publishers.
- Godfray, H. C. J. (1991). Signalling of need by offspring to their parents. *Nature*, 352, 328-330.
- Godfray, H. C. J. (1995a). Evolutionary theory of parent-offspring conflict. *Nature*, 376, 133-138.
- Godfray, H. C. J. (1995b). Signalling of need between parents and young: parent-offspring conflict and sibling rivalry. *American Naturalist*, 146, 1-24.
- Godfray, H. C. J. (1999). Parent-offspring conflict. In L. Keller (Ed.), *Levels of selection in evolution* (pp. 100-120). Princeton, New Jersey: Princeton University Press.
- Godfray, H. C. J., & Johnstone, R. A. (2000). Begging and bleating: the evolution of parent-offspring signalling. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 355, 1581-1591.
- Greenwood-Lee, J. M., Taylor, P. D., & Haig, D. (2001). The inclusive fitness dynamics of genomic imprinting. *Selection*, 2, 101-116.
- Hahn, D. C. (1981). Asynchronous hatching in the laughing gull: cutting losses and reducing sibling rivalry. *Animal Behavior*, 29, 421-427.
- Haig, D. (1990). Brood reduction and optimal parental investment when offspring differ in quality. *American Naturalist*, 136, 550-566.
- Hamilton, W. D. (1964). The genetical evolution of social behavior. I & II. *Journal of Theoretical Biology*, 7, 1-52.

- Hamilton, W. D. (1970). Selfish and spiteful behaviour in an evolutionary model. *Nature*, 228, 1218-1220.
- Hamilton, W. D. (1975). Innate social aptitudes of man: an approach from evolutionary genetics. In R. Fox (Ed.), *Biosocial Anthropology* (pp. 133-153). London: Malaby Press.
- Hardy, I. C. W. (Ed.). (2002). *Sex ratios: concepts and research methods*. Cambridge: Cambridge University Press.
- Herwig, R., Davis, J. N., & Sulloway, F. J. (2002). Parental investment: how an equity motive can produce inequality. *Psychological Bulletin*, 128, 728-745.
- Houston, A. I. (1995). Parental effort and paternity. *Animal Behavior*, 50, 1635-1644.
- Houston, A. I., & Davies, N. B. (1985). The evolution of cooperation and life-history in the dunnock. In R. M. Sibly & R. H. Smith (Eds.), *Behavioral ecology: ecological consequences of adaptive behavior* (pp. 471-488). Oxford: Blackwell Scientific Publications.
- Houston, A. I., & McNamara, J. M. (1999). *Models of adaptive behaviour*. Cambridge: Cambridge University Press.
- Johnstone, R. A. (2004). Begging and sibling competition: how should offspring respond to their rivals? *American Naturalist*, 163, 388-406.
- Judd, C. M., & McClelland, G. H. (1989). *Data analysis: A model comparison approach*. San Diego, CA: Harcourt Brace Jovanovich, Inc.
- Kaplan, H. S., & Gangestad, S. W. (2005). Life history theory and evolutionary psychology. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 68-95). Hoboken, New Jersey: John Wiley & Sons, Inc.
- Kilner, R. (1995). When do canary parents respond to nestling signals of need? *Proceedings of the Royal Society of London, Series B*, 260, 343-348.
- Kilner, R., & Johnstone, R. A. (1997). Begging the question: are offspring solicitation behaviors signals of needs? *Trends in Ecology & Evolution*, 12, 11-15.
- Korchmaros, J. D., & Kenny, D. A. (2001). Emotional closeness as a mediator of the effect of genetic relatedness on altruism. *Psychological Science*, 12(3), 262-265.
- Korchmaros, J. D., & Kenny, D. A. (2006). An evolutionary and close-relationship model of helping. *Journal of Social and Personal Relationships*, 23(1), 21-43.
- Kowal, A., & Kramer, L. (1997). Children's understanding of parental differential treatment. *Child Development*, 68(1), 113-126.
- Kowal, A., Kramer, L., Krull, J. L., & Crick, N. R. (2002). Children's perceptions of the fairness of parental preferential treatment and their socioemotional well-being. *Journal of Family Psychology*, 16(3), 297-306.

- Kowal, A., Krull, J. L., & Kramer, L. (2004). How the differential treatment of siblings is linked with parent-child relationship quality. *Journal of Family Psychology*, 2004(18(4)), 658-665.
- Krebs, E. A., Cunningham, R. B., & Donnelly, C. F. (1999). Complex patterns of food allocation in asynchronously hatching broods of crimson rosellas. *Animal Behavior*, 57, 753-763.
- Kurland, J. A., & Gaulin, S. J. C. (2005). Cooperation and competition among kin. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 447-482). Hoboken, N.J.: John Wiley & Sons.
- Lack, D. (1947). The significance of clutch size. *Ibis*, 89, 302-352.
- Lack, D. (1954). *The Natural regulation of animal numbers*. Oxford: Oxford University Press.
- Laham, S. M., Gonsalkorale, K., & von Hippel, W. (2005). Darwinian grandparenting: preferential investment in more certain kin. *Personality and Social Psychology Bulletin*, 31(1), 63-72.
- Leimar, O. (2001). Evolutionary change and Darwinian demons. *Selection*, 2, 65-72.
- Leimar, O. (2005). The evolution of phenotypic polymorphism: randomized strategies versus evolutionary branching. *American Naturalist*, 165, 669-581.
- Leimar, O. (in press). Multidimensional convergence stability and the canonical adaptive dynamics. In U. Dieckmann & J. A. J. Metz (Eds.), *Elements of adaptive dynamics*. Cambridge: Cambridge University Press.
- Leonard, M., & Horn, A. (1996). Provisioning rules in tree swallows. *Behavioral Ecology and Sociobiology*, 38(341-347).
- Levi-Strauss, C. (1969). *The elementary structures of kinship*. Boston: Beacon.
- Lloyd, D. G. (1985). Parallels between sexual strategies and other allocation strategies. *Experientia*, 41, 1277-1285.
- Lloyd, D. G. (1988). A general principle for the allocation of limited resources. *Evolutionary Ecology*, 2, 175-187.
- Lotem, A. (1998). Higher levels of begging behavior by small nestlings: a case of a negatively correlated handicap. *Israel Journal of Zoology*, 44, 29-45.
- Macnair, M. R., & Parker, G. A. (1979). Models of parent-offspring conflict. III. Intra-brood conflict. *Animal Behavior*, 26, 111-122.
- Magrath, R. D. (1990). Hatching asynchrony in altricial birds. *Biological Reviews*, 65, 587-622.
- Marlowe, F. (1999). Male care and mating effort among Hazda foragers. *Behavioral Ecology and Sociobiology*, 46, 57-64.
- Maynard Smith, J. (1982). *Evolution and the theory of games*. Cambridge ; New York: Cambridge University Press.

- Maynard Smith, J., & Price, G. (1973). The logic of animal conflicts. *Nature*, *246*, 15-18.
- McBurney, D. H., Simon, J., Gaulin, S. J. C., & Geliebter, A. (2002). Matrilateral biases in the investment of aunts and uncles: Replication in a Population Presumed to Have High Paternity Certainty. *Human Nature*, *13*, 391-402.
- Messick, D. M. (1993). Equality as a decision heuristic. In B. A. Mellers & J. Baron (Eds.), *Psychological perspectives on justice: Theory and applications* (pp. 11-31). New York: Cambridge University Press.
- Metz, J. A. J., Nisbet, R. M., & Geritz, S. A. H. (1992). How should we define 'fitness' for general ecological scenarios? *Trends in Ecology & Evolution*, *7*, 198-202.
- Michalski, R. L., & Shackelford, T. K. (2005). Grandparental Investment as a Function of Relational Uncertainty and Emotional Closeness with Parents. *Human Nature*, *16*(3), 293-305.
- Mock, D. W., & Parker, G. A. (1997). *The evolution of sibling rivalry*. Oxford ; New York: Oxford University Press.
- Mock, D. W., & Ploger, B. J. (1987). Parental manipulation of optimal hatch asynchrony in cattle egrets: an experimental study. *Animal Behavior*, *35*(150-160).
- Mylius, S. D., & Diekmann, O. (1995). On evolutionarily stable life histories, optimization and the need to be specific about density dependence. *Oikos*, *74*, 218-224.
- Neyer, F. J., & Lang, F. R. (2003). Blood is thicker than water: kinship orientation across adulthood. *Journal of personality and social psychology*, *84*(2), 310-321.
- Otto, S. P., & Day, T. (2007). *A Biologist's Guide to Mathematical Modeling in Ecology and Evolution*. Princeton, NJ: Princeton University Press.
- Parker, G. A., & Macnair, M. R. (1979). Models of parent-offspring conflict. IV. Suppression: evolutionary retaliation by the parent. *Animal Behavior*, *27*, 1210-1235.
- Parker, G. A., Mock, D. W., & Lamey, T. C. (1989). How selfish should stronger sibs be? *American Naturalist*, *133*, 846-868.
- Parker, G. A., Royle, N. J., & Hartley, I. R. (2002a). Begging scrambles with unequal chicks: interactions between need and competitive ability. *Ecology Letters*, *5*, 206-215.
- Parker, G. A., Royle, N. J., & Hartley, I. R. (2002b). Intrafamilial conflict and parental investment: a synthesis. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, *357*, 295-307.
- Pashos, A. (2000). Does paternity uncertainty explain discriminative grandparental solicitude? A cross cultural study in Greece and Germany. *Evolution and Human Behavior*, *21*, 97-109.

- Pen, I., & Weissing, F. J. (2000). Towards a unified theory of cooperative breeding: the role of ecology and life history re-examined. *Proceedings of the Royal Society of London, Series B*, *267*, 2411-2418.
- Pen, I., & Weissing, F. J. (2002). Optimal sex allocation: steps towards a mechanistic theory. In I. Hardy (Ed.), *Sex ratios : concepts and research methods* (pp. 26-45). New York: Cambridge University Press.
- Price, K., Harvey, H., & Ydenberg, R. (1996). Begging tactics of nestling yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. *Animal Behavior*, *51*, 421-435.
- Price, K., & Ydenberg, R. (1995). Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. *Behavioral Ecology and Sociobiology*, *37*, 201-208.
- Ricklefs, R. E. (2000). Density dependence, evolutionary optimization, and the diversification of avian life histories. *Condor*, *102*, 9-22.
- Rodriguez-Girones, M. A. (1999). Sibling competition stabilizes signalling resolution models of parent-offspring conflict. *Proceedings of the Royal Society of London, Series B*, *266*, 2399-2402.
- Rodriguez-Girones, M. A., Cotton, P. A., & Kacelnik, A. (1996). The evolution of begging: signaling and sibling competition. *Proceedings of the National Academy of Sciences, USA*, *93*, 14627-14641.
- Rodriguez-Girones, M. A., Enquist, M., & Lachmann, M. (2001). Role of begging and sibling competition in foraging strategies of nestlings. *Animal Behaviour*, *61*, 733-745.
- Rohde, P. A., Atzwanger, K., Butovskaya, M., Lampert, A., Mysterud, I., Sanchez-Andres, A., et al. (2003). Perceived parental favoritism, closeness to kin, and the rebel of the family: the effects of birth order and sex. *Evolution and Human Behavior*, *24*, 261-276.
- Royle, N. J., Hartley, I. R., & Parker, G. A. (2002). Begging for control: when are offspring solicitation behaviors honest? *Trends in Ecology & Evolution*, *17*, 434-440.
- Rubenstein, D. I. (1982). Reproductive value and behavioral strategies: coming of age in monkeys and horses. *Perspectives in Ethology*, *5*, 469-487.
- Salmon, C. A. (1999). On the impact of sex and birth order on contact with kin. *Human Nature*, *10*, 183-197.
- Salmon, C. A. (2005). Parental investment and parent-offspring conflict. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 506-527). Hoboken, N. J.: John Wiley & Sons.
- Salmon, C. A., & Daly, M. (1998). Birth order and familial sentiment: Middleborns are different. *Evolution and Human Behavior*, *19*, 299-312.

- Sargent, R. C., & Gross, M. R. (1986). William's principle: an explanation of parental care in teleost fishes. In T. Pitcher (Ed.), *The behavior of teleost fishes* (pp. 275-293). London: Croom Helm Publishers.
- Sears, R., Mace, R., & McGregor, I. (2000). Maternal grandmothers improve nutritional status and survival of children in rural Gambia. *Proceedings of the Royal Society, B: Biological Sciences*, *267*, 1641-1647.
- Simpson, J. A., & Kenrick, D. T. (1997). *Evolutionary social psychology*. Mahwah, N.J.: Lawrence Erlbaum Associates.
- Smiseth, P. T., & Amundsen, T. (2002). Senior and junior nestlings in asynchronous bluethroat broods differ in their effectiveness of begging. *Evolutionary Ecology Research*, *4*, 1177-1189.
- Smiseth, P. T., Bu, R. J., Erikenaes, A. K., & Amundsen, T. (2003). Food limitation in asynchronous bluethroat broods: effects on food distribution, nestling begging, and parental provisioning rules. *Behavioral Ecology*, *14*, 793-801.
- Smith, C. C., & Fretwell, S. D. (1974). The optimal balance between size and number of offspring. *American Naturalist*, *108*, 499-506.
- Smith, M. S. (1988). Research in developmental sociobiology: parenting and family behavior. In K. B. MacDonald (Ed.), *Sociobiological perspectives on human development* (pp. 271-292). New York: Springer.
- Stamps, J., Clark, A., Arrowood, P., & Kus, B. (1985). Parent-offspring conflict in budgerigars. *Behaviour*, *94*, 1-40.
- Stocker, C. M., Dunn, J., & Plomin, R. (1989). Sibling relationships: Links with child temperament, maternal behavior, and family structure. *Child Development*, *60*, 715-727.
- Sulloway, F. J. (1996). *Born to rebel: Birth order, family dynamics, and creative lives*. New York: Pantheon Books.
- Sulloway, F. J. (2001). Birth order, sibling competition, and human behavior. In H. R. Holcomb III (Ed.), *Conceptual challenges in evolutionary psychology: Innovative research strategies* (pp. 39-83). Dordrecht, the Netherlands: Kluwer Academic Publishers.
- Taylor, P. D. (1990). Allele frequency change in a class-structured population. *American Naturalist*, *135*, 95-106.
- Taylor, P. D. (1996). Inclusive fitness arguments in genetic models of behaviour. *Journal of Mathematical Biology*, *34*, 654-674.
- Taylor, P. D., & Frank, S. A. (1996a). How to make a kin selection model. *Journal of Theoretical Biology*, *180*, 27-37.
- Taylor, P. D., & Frank, S. A. (1996b). How to make a kin selection model. *Journal of Theoretical Biology*, *180*, 27-37.

- Taylor, P. D., Wild, G., & Gardner, A. (2006). Direct fitness or inclusive fitness: how shall we model kin selection? *Journal of Evolutionary Biology*, 20(1), 1-9.
- Temme, D. H. (1986). Seed size variability: a consequence of variance genetic quality among offspring? *Evolution*, 40, 414-417.
- Trivers, R. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 139-179). Chicago: Aldine Press.
- Trivers, R. (1974). Parent-offspring conflict. *American Zoologist*, 14, 249-264.
- West-Eberhard, M. J. (1975). The evolution of social behavior by kin selection. *Quarterly Review of Biology*, 50, 1-33.
- White, L. K., & Riedmann, A. (1992). Ties among adult siblings. *Social Forces*, 71, 85-102.
- Wild, G., & Taylor, P. D. (2004). Kin selection models for the co-evolution of the sex ratio and sex-specific dispersal. *Evolutionary Ecology Research*, 6, 481-502.
- Williams, G. C. (1966). *Adaptation and Natural Selection*. Princeton, NJ: Princeton University Press.
- Wilson, E. O. (1975). *Sociobiology*. Cambridge, Mass.: Belknap Press of Harvard University Press.
- Wilson, M., & Daly, M. (1997). Relationship-specific social psychological adaptations. In G. Bock & G. Cardew (Eds.), *Characterizing human psychological adaptations* (pp. 253-268). Chichester: Wiley.
- Winkler, D. W. (1987). A general model for parental care. *American Naturalist*, 130, 526-543.
- Wright, J., & Leonard, M. L. (2002). *The evolution of begging: competition, cooperation, and communication*. Dordrecht: Kluwer Academic Publishers.

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