Evolution of parental favoritism among different-aged offspring

Joonghwan Jeon
Department of Psychology, University of Texas at Austin, Austin, TX 78712, USA

The theories of intrafamilial conflict and parental investment have yet to examine how parents' decisions about resource allocation are influenced by the fact that their offspring may be different in age. Two counteracting effects of offspring growth on parental allocation of resources have deterred the development of a formal model: A parent may favor older offspring due to their greater reproductive value or favor younger offspring due to their higher marginal returns from extra resources. Using an 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 the parent. The parent's evolutionarily stable strategy is to allocate its resources such that 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. Two general situations are considered in which younger offspring obtain higher marginal returns than older offspring. In nearly all circumstances, a parent is expected to bias its resources toward older offspring. The results may account for the widespread yet puzzling phenomenon of parental bias toward older offspring in view of previous theories of intrafamilial conflict. *Key words:* evolutionarily stable strategy, hatching asynchrony, invasion analysis, offspring age, parental investment, reproductive value. *[Behav Ecol]*

$\mathbf{P}$arents are expected to adaptively allocate their limited resources among offspring so as to maximize parental fitness (Smith and Fretwell 1974; Winkler 1987; Clutton-Brock 1991). Yet offspring may be selected to demand more resources than parents are selected to provide (Trivers 1974), which leads to conflict among family members over the flow of parental investment. The 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 and Parker 1997). Initially, begging was interpreted as the outcome of scramble competition among nestlings, with the assumption of the offspring's full control over resource allocation (Macnair and Parker 1979; Parker and Macnair 1979). The alternative model suggests that begging displays honestly advertise the offspring's cryptic condition (defined as the offspring's marginal fitness gain from obtaining extra resources) to parents, who control resource allocation within broods (Godfray 1991, 1995). The honest signaling model predicts that parents should invest more in needier offspring, an idea that is supported by empirical evidence showing that hungrier nestlings do indeed beg more and receive more food from their parents (Kilner and Johnstone 1997).

Within-brood resource allocation, however, should be shaped not only by the offspring's cryptic internal condition (commonly called "need") but also by the offspring's external condition: information that parents may directly access, such as offspring age, sex, and competitive ability (Glassey and Forbes 2002). In particular, age differences among offspring are 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 higher mor-

tality 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 and Parker 1979; Parker and Macnair 1979). Yet, parents may have full or partial control over food distribution and preferentially invest in 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 (internal) and noncryptic (external) conditions of offspring affect family dynamics, it is necessary to elucidate the optimal distribution of resources among different-aged offspring from the viewpoint of parents.

Unfortunately, no formal investigations have been made about how parents should allocate resources among offspring of different ages (Clutton-Brock 1991). Making realistic predictions has been considered very difficult due to 2 potentially counteracting effects of offspring growth on the ES level of parental provisioning. Parents may favor older offspring because older offspring have higher reproductive value (i.e., should make a higher genetic contribution to future populations) (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 (Clutton-Brock 1991). On the other hand, parents may favor younger offspring because younger offspring have greater need for food than older offspring, so the effect of a unit of additional investment on offspring survival will be higher for younger offspring (Rubenstein 1982; Sargent and Gross 1986; Clutton-Brock 1991).

The results of recent empirical studies of food allocation in asynchronously hatched broods pose a serious problem for current models of parent–offspring interactions (Lotem 1998; Cotton et al. 1999; Smiseth and Amundsen 2002). According to the honest signaling model's definition of need, younger (smaller) nestlings are in greater need of food; hence, they should beg more vigorously and receive more food than older (larger) nestlings. However, many experimental studies have found that older nestlings actually receive more food, even though they beg less intensively than their

Address correspondence to J. Jeon, who is now at the Division of EcoScience, Ewha Womans University, Seoul 120-750, Republic of Korea. E-mail: evopsy@gmail.com.

younger siblings (Kilner 1995; Price et al. 1996; Lotem 1998; Cotton et al. 1999; Smiseth and Amundsen 2002). This striking discrepancy between theoretical predictions and empirical findings may indicate that fundamental aspects of parent–offspring interactions have yet to be understood (Cotton et al. 1999). Meanwhile, the scramble competition model assumes that offspring fully control food allocation within broods and predicts that older offspring with higher competitive ability should get more food than younger offspring, which is consistent with most observed allocation patterns in asynchronously hatched broods (Mock and Parker 1997; Parker et al. 2002). However, there remains the possibility that parents may have partial or full control over food distribution and actively prefer feeding older offspring. Indeed, recent empirical evidence suggests that parents may play an active role in food allocation within asynchronous broods (Kilner 1995; Krebs et al. 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 and fecundity on a common scale (Taylor 1990; Charlesworth 1994; Taylor and Frank 1996; Frank 1998; Pen and Weissing 2002). After envisioning a genetically homogeneous population with a fixed allocation strategy among offspring of different age classes, one can determine whether the resident population can be invaded by a rare mutant allocation strategy. This approach can reveal the outcome of long-term evolution and has been recently referred to as an evolutionary invasion analysis (for a clear introduction, see Otto and Day 2007). Assuming parental control over resource allocation, I present a model that investigates how a parent should invest in offspring of different age classes. Within the model's life-history framework based on reproductive value, the effect of additional food on the survival of younger offspring will be allowed to be higher than the effect on survival of older offspring. The model presented here thus integrates the 2 counteracting effects of offspring growth on parental allocation strategies within broods.

THE MODEL

Dynamics of resident population

Consider a diploid resident population that is structured into parents (class P) and their offspring, which are classified into n age classes (class $O_i : i = 1, \ldots, n$). For the sake of simplicity, the model employs hermaphroditic individuals that reproduce as both males and females. During a time step, an individual parent mates with another adult, producing f newborn offspring, allocates its limited resources among its different-aged offspring, and survives to the next time step with probability ψ. The population is further structured into distinct broods, for which each parent provisions only its own offspring within the brood. The length of the time step corresponds to the average age gap between offspring age classes; 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 period of time, it would be desirable to consider dynamic aspects of parent–offspring interactions as well. Unfortunately, such an analysis is extremely difficult to carry out. Following other authors (e.g., Parker et al. 1989; Godfray 1991, 1995; Rodríguez-Gironés et al. 1996; Johnstone 2004), I assume that, for each time step,
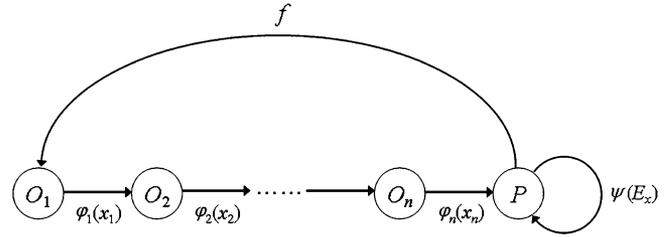

Figure 1
A life cycle graph for an age-structured population with a parental class and n different-aged offspring classes. The arcs indicate transitions between age classes; the symbols labeling each arc indicate the contribution of each age class to another.

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 overall allocation strategy.

When a focal parent invests in its current brood composed of different-aged offspring, it suffers a cost in terms of reduced 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 (it is assumed that parents can discriminate between offspring of differing ages with negligible cost). Thus, the total amount of resources that an average parent provides for its current brood per 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 $\mathbf{x} = [x_1, x_2, \ldots, x_n]$, 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 $i + 1$ with survival probability $\varphi_i = \varphi_i(x_i)$, an increasing function of x_i. A focal parent's survival probability into the next time step is $\psi(E_x)$, a decreasing function of E_x. Figure 1 depicts the life cycle for the resident population. The population transition matrix $\mathbf{A}$ corresponding to Figure 1 is

$$\mathbf{A} = \begin{bmatrix} 0 & 0 & \cdots & 0 & f \\ \varphi_1(x_1) & 0 & \cdots & 0 & 0 \\ 0 & \varphi_2(x_2) & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & \varphi_n(x_n) & \psi(E_x) \end{bmatrix}. \quad (1)$$

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 $\mathbf{u}^* = [u_1^*, u_2^*, \ldots, u_n^*, u_p^*]$ is the dominant right eigenvector of $\mathbf{A}^*$. Because $\mathbf{u}^*$ is determined up to a constant, I let the number of parental class u_p^* equals 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 $\mathbf{v}^* = [v_1^*, v_2^*, \ldots, v_n^*, v_p^*]$ is the dominant left eigenvector of $\mathbf{A}^* : \mathbf{v}^* \mathbf{A}^* = \lambda \mathbf{v}^*$. The 2 vectors $\mathbf{u}^*$ and $\mathbf{v}^*$ are obtained in Appendix A.

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 that the following equation be satisfied

$$f \varphi_1(x_1^*) \varphi_2(x_2^*) \cdots \varphi_n(x_n^*) = 1 - \psi(E_x^*), \quad (2)$$

where $E_x^* = \sum_{i=1}^{n} u_i^* x_i^*$. Equation 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 it should be decided which vital rate in the life cycle will be influenced by the population density (Mylius and Diekmann 1995; Pen and Weissing 2000, 2002). Because 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 is satisfied (in this system, it does not make any difference if I choose other vital rates to be density dependent).

One may suspect that the resident matrix $\mathbf{A}$ in Equation 1 does not accurately describe the actual population that it is meant to. In order for a newborn age-1 offspring to become an age-$(n + 1)$ adult, it should be continually cared for by its living parent throughout n time steps (as implied in $\varphi_1(x_1), \ldots, \varphi_n(x_n)$), yet the matrix $\mathbf{A}$ also assumes that there will be a nonzero parental mortality $1 - \psi(E_x)$ for each time step. In other words, although the model assumes that each and every age-i offspring will receive x_i from the parents and survive to the next time step with probability $\varphi_i(x_i)$, it seems that some offspring will never receive x_i because they would lose their parents across time. Appendix B clarifies this issue and shows that each and every age-i offspring can be regarded as receiving x_i from its living parent at any time step.

Invasion analysis

To find the ES allocation strategy among different-aged offspring, I seek to determine under what conditions a rare mutant allocation strategy $\mathbf{x}^\circ(= [x_1^\circ, \ldots, x_n^\circ]$, where $x_i^\circ = x_i + \Delta x)$ can invade the resident population fixed for the resident strategy $\mathbf{x}^*$. The mutant strategy $\mathbf{x}^\circ$ is assumed to be rare enough that the average number of age-i offspring per mutant adult is given by u_i^*, that is, the offspring's age distribution in the resident population with $\mathbf{x}^*$ (with the rarity assumption, the eigenvectors of the resident population, i.e., $\mathbf{u}^*$ and $\mathbf{v}^*$, can be used to characterize the mutant dynamics. See Taylor and Frank [1996, p. 36] for the proof). The transition matrix of the mutant subpopulation is

$$\mathbf{A}(\mathbf{x}^\circ, \mathbf{x}^*) = \begin{bmatrix} 0 & 0 & \cdots & 0 & f \\ \varphi_1(x_1^\circ) & 0 & \cdots & 0 & 0 \\ 0 & \varphi_2(x_2^\circ) & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & \varphi_n(x_n^\circ) & \psi(E_x^\circ) \end{bmatrix}, \quad (3)$$

where $E_x^\circ = \sum_{i=1}^n u_i^* x_i^\circ = \sum_{i=1}^n f \varphi_1^* \varphi_2^* \cdots \varphi_{i-1}^* x_i^\circ$ (see Appendix A).

The invasion fitness of a mutant strategy $\mathbf{x}^\circ$ is sought as the initial growth rate of the mutant subpopulation within the resident population, that is, 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 $\mathbf{x}^\circ$ to be ES, $\lambda(\mathbf{x}^\circ, \mathbf{x}^*)$ should have a local maximum at $\mathbf{x}^\circ = \mathbf{x}^*$ such that

$$\left. \frac{\partial \lambda(\mathbf{x}^\circ, \mathbf{x}^*)}{\partial \mathbf{x}^\circ} \right|_{\mathbf{x}^\circ = \mathbf{x}^*} = 0 \quad (4)$$

and the Hessian matrix of $\lambda(\mathbf{x}^\circ, \mathbf{x}^*)$ is negative semidefinite (i.e., all its eigenvalues are less than or equal to zero) at the equilibrium point $(x_1^*, \ldots, x_n^*)$ (Day and Taylor 2003). The first-order condition for a strategy $\mathbf{x}^*$ to be an evolutionarily

stable strategy (ESS) can be rewritten as the following n equations:

$$\left. \mathbf{v}^* \frac{\partial \mathbf{A}(\mathbf{x}^\circ, \mathbf{x}^*)}{\partial x_i^\circ} \right|_{x_i^\circ = x_i^*} \mathbf{u}^* = 0 \ (i = 1, \ldots, n). \quad (5)$$

Note that although the correct fitness measure of a rare mutant strategy $\mathbf{x}^\circ$ is $\lambda(\mathbf{x}^\circ, \mathbf{x}^*)$, one 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 and Frank 1996). From Equation 5 and Appendix A, a parent's ES allocation strategy $\mathbf{x}^*(= [x_1^*, \ldots, x_n^*])$ is obtained by n equilibrium conditions as follows:

$$(\varphi_2^* \varphi_3^* \cdots \varphi_n^*) \varphi_1'(x_1^*) = -\psi'(E_x^*)$$
$$(\varphi_3^* \cdots \varphi_n^*) \varphi_2'(x_2^*) = -\psi'(E_x^*)$$
$$\vdots$$
$$\varphi_n'(x_n^*) = -\psi'(E_x^*), \quad (6)$$

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 6 indicates that, at the ES allocation from a parent's viewpoint, the marginal benefit from additional resources for each offspring's survival $\varphi_i'(x_i^*)$, weighted by the survival probability of each offspring to reproductive age (i.e., $\varphi_{i+1}^* \varphi_{i+2}^* \cdots \varphi_n^*$), 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 verified in Appendix C.

RESULTS

To derive concrete predictions about the parental ES allocation of resources among different-aged offspring, I allow the effect of additional resources on the survival of younger offspring to be greater than the effect on the survival of older offspring, in accordance with previous research (West-Eberhard 1975; Rubenstein 1982; Sargent and Gross 1986; Clutton-Brock 1991). There are 2 general situations where a younger offspring would have a greater need for food than an older offspring. First, the marginal benefit from additional resources may be always higher for younger offspring than older offspring, regardless of resources already provided during a given feeding bout. Alternatively, the marginal benefit from additional resources may be higher for younger offspring only when resources already provided are none or few (i.e., when both offspring are hungry and equally so); if the resources already provided are relatively high (i.e., when both offspring are well fed and equally so), the marginal gain from 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 almost never increase with additional resources, whereas the former's survival will still slightly increase. The second situation appears more plausible and has been assumed by previous researchers (Rubenstein 1982; Sargent and Gross 1986; Clutton-Brock 1991). In both situations, I assume that a parent completely controls both the total amount of resources delivered and the division of the resources among 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., $\varphi'(x) > 0$, $\varphi''(x) < 0$) (Smith and Fretwell 1974). Consider 2 offspring spaced by 1 time step. At evolutionary equilibrium, each offspring will receive its ES level of resources (i.e., x_i^* and x_{i+1}^*, where $i = 1,\ldots, n - 1$) from the parent. Because $\varphi'(x)$ decreases with 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 $\delta(x_{i+1}^*)$. Note that $\delta(x_{i+1}^*)$ can be regarded as a function of x_{i+1}^* only; the equilibrium conditions in Equation 6 imply that I can rewrite $\varphi_i'(x_i^*) - \varphi_i'(x_{i+1}^*)$ as

$$\delta(x_{i+1}^*) = \varphi_i'(x_i^*) - \varphi_i'(x_{i+1}^*) = \frac{\varphi_{i+1}'(x_{i+1}^*)}{\varphi_{i+1}'(x_{i+1}^*)} - \varphi_i'(x_{i+1}^*). \quad (7)$$

The sign of $\delta(x_{i+1}^*)$ informs whether x_i^* is larger or smaller than x_{i+1}^*. For instance, a plus sign 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 $\delta(x_{i+1}^*) = \varphi_i'(x_i^*) - \varphi_i'(x_{i+1}^*) > 0$ for all levels of x (see Appendix D for the proof). Because $\varphi'(x)$ 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 $\mathbf{x}^*$ ($=[x_1^*,\ldots, x_n^*]$) is to distribute its resources such that older offspring get more resources than younger offspring (i.e., $x_1^* < x_2^* < \cdots < x_n^*$).

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

$$\varphi_i(x_i) = K_i[1 - \exp(-cx_i)], \quad (8)$$

where K_i is a positive constant denoting the asymptotic level of offspring survival ($0 < K_i \le 1$) and c, a 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 $\varphi_i'(x_i^*) > \varphi_i'(x_{i+1}^*)$ for every value of x (Figure 2a). In other words, the asymptote K_i of an age-i offspring survival curve will be inversely related to the offspring's age: $K_1 > K_2 > \ldots > K_n$. Throughout this paper, 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):

$$\psi(E_x) = G - a \exp(bE_x) = G - a \exp\left(b \sum_{i=1}^{n} u_i^* x_i \right), \quad (9)$$

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 2 offspring is given in Figure 2b. In spite 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 off-
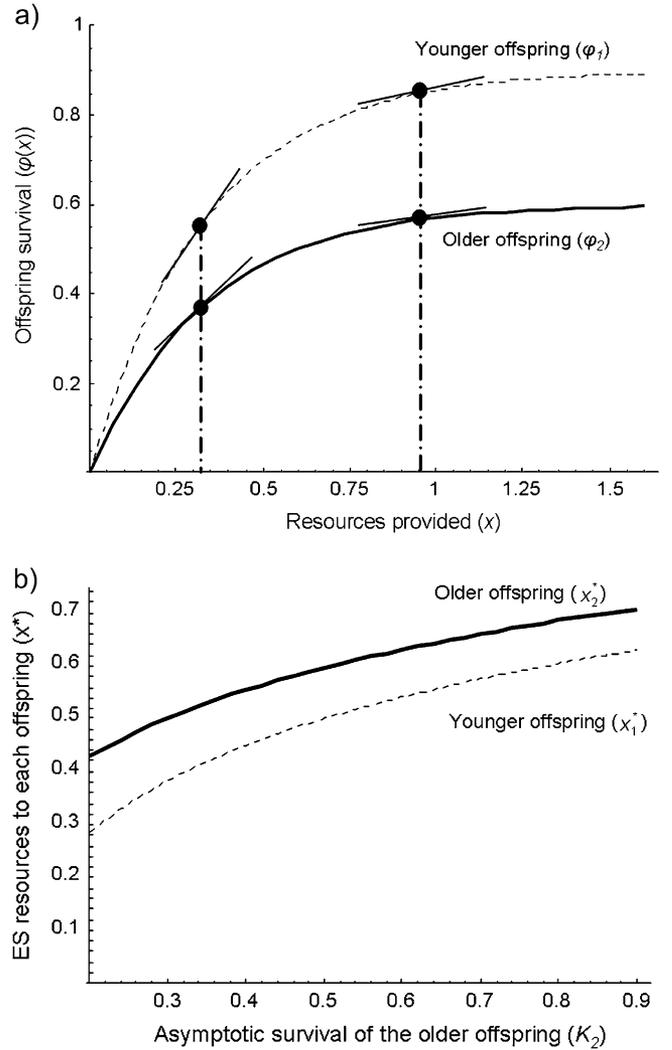

Figure 2

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 varies and the younger offspring's asymptote K_1 is fixed at 0.9. The equilibrium values were obtained from Equation 6 for 2 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 $b = 1$.

spring (i.e., the larger the age spacing between the 2 offspring), the more favored the older offspring.

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 $\delta(x_{i+1}^*) = \varphi_i'(x_i^*) - \varphi_i'(x_{i+1}^*)$ is positive and hence $x_i^* < x_{i+1}^*$ (see Appendix E 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., $x_1^* < x_2^* < \cdots < x_n^*$).

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

$$\varphi_i(x_i) = K_i[1 - \exp(-c_i x_i)], \qquad (10)$$

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: $c_1 > c_2 > \ldots > c_n$ (Figure 3a) (Sargent and Gross 1986; Clutton-Brock 1991). This is consistent with the honest signaling model's assumption that the survival curve of "needier" (hence younger) offspring is regarded as having a greater c value, yet the honest signaling model (incorrectly) contends that younger offspring yield a higher marginal return no matter what value of x is provided (Godfray 1991, 1995).

Figure 3b gives the ES allocation of resources between 2 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 when no or few resources have been provided, the parent will preferentially invest in the older offspring throughout the range of the older offspring's shape constant c_2 (i.e., whenever there is any age difference between the 2 offspring). The graph also reveals that as c_2 decreases, whereas c_1 is fixed (hence, as the older offspring's age increases relative to the younger offspring's fixed age), the older offspring's resource share increases and the younger offspring's resource share, to a lesser extent, decreases. In other words, the larger the age spacing between 2 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 (Appendix E). On the other hand, it can be argued that 2 different-aged offspring will differ in the minimum threshold levels of resources at which their survival probabilities start increasing, hereafter referred to as the "threshold level of resources." For instance, older offspring will tend to have larger body sizes, thus requiring a higher threshold level of resources than the younger offspring. I investigated the consequence of different threshold levels of resource requirements between siblings. The analysis revealed that parents will still bias their resource allocation 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 be favored if the younger offspring's threshold is sufficiently greater than the older offspring's one; yet it is difficult to imagine how a younger offspring's threshold level of resources could be higher than the older offspring's one in natural populations.

DISCUSSION

Using an evolutionary invasion analysis of class-structured populations, the current model examined 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. After previous discussions, I considered 2 general situations in which younger offspring obtain a higher
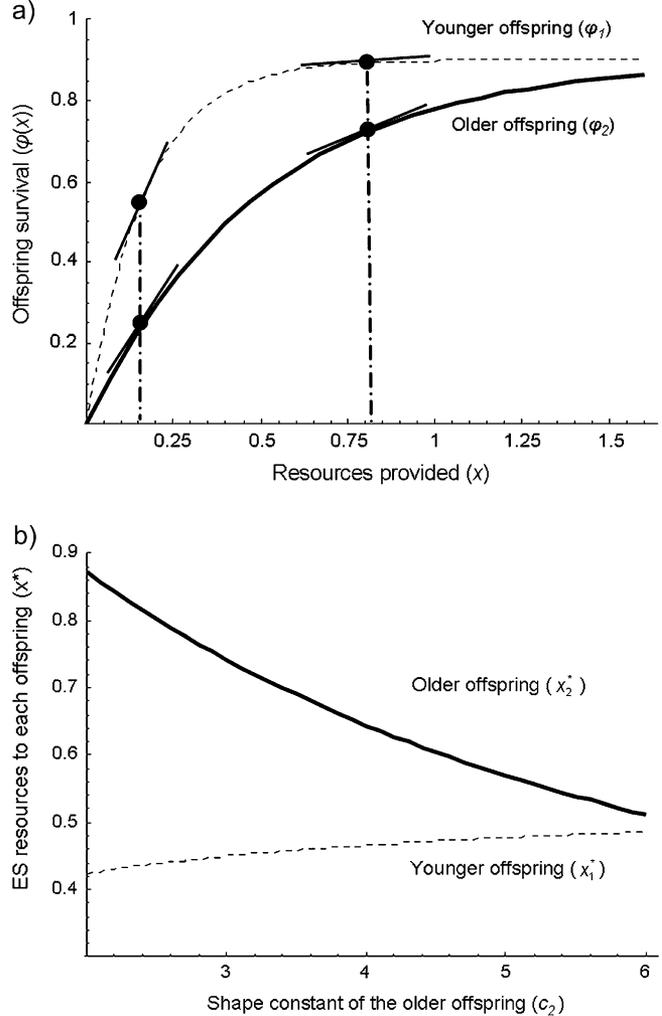

Figure 3
A situation in which a younger offspring yields higher marginal returns than an older offspring only when the amount of resources provided is none or few. (a) The survival probabilities of each offspring ($\varphi(x)$) as a function of the resources provided (x) during a single feeding episode. 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 and the younger offspring's shape constant c_1 is fixed at 6. The equilibrium values were obtained from Equation 6 for 2 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 $b = 1$.

marginal return from additional resources than older offspring. The model predicted that a parent should bias its resources in favor of older offspring in nearly all circumstances and that the degree of parental favoritism will increase as the age spacing between 2 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 (Lloyd 1985, 1988; Temme 1986; Haig 1990; Lessells 2002). 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: $\varphi_1'(x_1^*) = \varphi_2'(x_2^*) = \cdots = \varphi_n'(x_n^*) = -\psi(x_1^* + \cdots + x_n^*)$, where $\varphi'i(x_i^*)$ is the marginal gain in terms of offspring's survival from investment in an age-i offspring and $\psi'(x_1^* + \cdots + x_n^*)$ 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 in each offspring's survival weighted by the probability of survival to reproductive age (see Equation 6). In this scheme, the consequences of the parental actor's investment in recipient offspring structured into different age classes are measured on a common scale, that is, the extent to which current investment in an age-i offspring eventually contributes to that offspring's growth into a reproducing adult. Interestingly, due to the weighting by the survival probability to reproductive age, the marginal gain from investment in a younger offspring must be higher than that from investment in an older offspring at the parental ESS: $\varphi_1'(x_1^*) > \varphi_2'(x_2^*) > \cdots > \varphi_n'(x_n^*) = -\psi'(E_1^*)$ (see Equation 7, 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 traditional allocation theory, which insists on the equilibration of marginal gains across all offspring at ESS, the model presented here sheds new light on 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 investment in younger offspring will be greater than those from investment in older offspring at the parental ESS. What are equalized in this case are the marginal gains from each offspring weighted by the offspring's probability of survival to reproductive 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 (Kilner 1995; Price et al. 1996; Lotem 1998; Cotton et al. 1999; Smiseth and Amundsen 2002).

One may wonder to what extent the main result of the current model, that is, biased allocation of parental resources toward older offspring, depends on the assumption of higher marginal benefits for younger offspring. Remarkably, the result is fairly robust even under the opposite assumption. If investment in an older offspring yields higher marginal returns for any level of resources already provided, then the model predicts that the parent will favor the older offspring. If investment in the older offspring yields higher marginal returns only when no or few resources have already been provided, then a parent will also favor the older offspring on the condition that the age gap between 2 offspring is relatively small (Jeon J, unpublished data). These insights suggest that the results presented here may be widely applicable across a variety of family systems.

Implications for models of intrafamilial conflict

The 2 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 from 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 from additional resources than older offspring under 2 different sets of conditions. Consequently, the model presented here disentangles and integrates the 2 counteracting effects of offspring growth on parental allocation of resources.

Under nearly all circumstances, the model generates a clear-cut prediction that a parent will preferentially invest in older offspring over younger offspring. An exceptional allocation favoring younger offspring is possible only when the younger offspring's threshold level of resources is sufficiently greater than that of the older offspring, which is likely to 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., Leonard and Horn 1996; Krebs et al. 1999; Stamps et al. 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 a widespread yet enigmatic phenomenon observed in most asynchronously hatching birds: Younger nestlings indeed receive less food than older nestlings, even though the former beg more intensively (Kilner 1995; Price and Ydenberg 1995; Price et al. 1996; Lotem 1998; Cotton et al. 1999; Smiseth and Amundsen 2002). Existing models of parent–offspring interactions, lacking in formal analysis of class-structured populations, have failed to explain this phenomenon. In particular, the honest signaling model predicts that parents should bias their resources toward the needier (i.e., younger) offspring, which runs counter to abundant empirical data. The model presented here provides a straightforward solution for this hitherto unresolved problem.

In addition to the lack of formal analysis of class-structured populations, the honest signaling model suffers from a conceptual problem in defining offspring's cryptic condition (or need) in terms of the shape constant c of offspring's survival functions. In such models, needier offspring (hungrier offspring in the short term; younger [smaller] offspring in the long term) correspond to those yielding a higher marginal gain from additional resources (i.e., $\partial\varphi/\partial x$) (Price et al. 1996). Unfortunately, in presenting an explicit example for their analysis, the honest signaling theorists assumed that needier offspring correspond to those having a lower value of c in their survival functions compared with their siblings (Godfray 1991, 1995). In reality, as the Results section shows, the c values of survival curves do not reliably reflect marginal gains from extra resources ($\partial\varphi/\partial x$): A survival curve with a higher c value may yield either a higher or lower marginal gain than a curve with a lower c value, depending on the amount of resources, x, already provided (see Figure 3a) (Parker et al. 2002; Royle et al. 2002). Hence, in the honest signaling model's terminology, younger offspring should not be regarded as being always needier because they will obtain a higher marginal return only when the resources already provided are none or few. Future research should focus on clarifying ambiguous terms like offspring need and "condition" found in current literature.

Limitations and conclusions

Several limitations of the present study should be noted. First, the current model assumes that parents always win the parent–offspring conflict and, hence, that the amount of resources transferred in nature is at the parental optimum. Yet the optimal resource allocations from the perspective of each different-aged offspring will differ, and it is possible that

offspring may (at least partly) win the parent–offspring conflict. Future research should address how the evolutionary conflict among various family members is resolved within an age-dependent life-history context. Second, 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. Third, like other models of parent–offspring interactions (e.g., Godfray 1995; Parker et al. 2002), the present model implicitly assumes that environmental conditions are favorable throughout the investment period and, hence, that enough food is available to be divided among all offspring. Yet empirical evidence suggests that parental provisioning decisions may be contingent on food availability (e.g., Boland et al. 1997; Kilner 2002; Bize et al. 2006). To address this issue, the current model should be expanded to include the effect of food availability. Fourth, the current model assumed hermaphroditic populations to avoid the complexity resulting from dioecy. Although the results obtained here should apply well to dioecious populations, it must be recognized that most birds have biparental care and the 2 parents can follow different allocation rules (Lessells 2002).

Theories of intrafamilial conflict, by their very nature, deal with social interactions between individuals of different classes; yet researchers have been slow to explicitly model the evolution of class-structured populations. The class-structured model presented here asked how a parental actor's behavior is influenced 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 a hitherto puzzling phenomenon observed in nature, which suggests that the study of intrafamilial interactions should benefit from the application of evolutionary invasion analysis in class-structured populations.

APPENDIX

A. Reproductive values and stable age distribution

Assuming that λ remains at 1 due to density-dependent regulation, the vector of individual reproductive values $\mathbf{v}^* = [v_1^*, \ldots, v_n^*, v_p^*]$ in the resident population can be determined up to a scalar constant from the recurrence equation $\mathbf{v}^*\mathbf{A}^* = \mathbf{v}^*$. Because 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

$$v_i^* = \prod_{k=i}^{n} \varphi_k^* \quad (i = 1, \ldots, n). \tag{A1}$$

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

$$u_i^* = f \prod_{k=i}^{i-1} \varphi_k^* \quad (i = 2, \ldots, n) \tag{A2}$$

and u_1 is defined as f.

B. The internal consistency of the resident matrix A

For simplicity, I consider a population in which offspring are classified into 2 age classes. Suppose that the age-structured population has just reached a stable age structure at time t. Let the total number of adults in the population be N (i.e., the population is divided into N broods). The numbers of individuals in age-1 and age-2 offspring classes are Nf and $Nf\varphi_1$, respectively (see Equation A2). Clearly, each age-i offspring in this population will receive x_i resources.

At time $t + 1$, $N\psi$ adults will survive and continue to provision their offspring. By contrast, $N(1 - \psi)$ adults will die, and hence, $N(1 - \psi)$ territories will become vacant. The model reasonably assumes that the death of a parent at any time step will immediately result in the death of all immature offspring in the brood. The newly recruited $Nf\varphi_1\varphi_2$ adults, who were age-2 offspring in the previous time step, will occupy the $N(1 - \psi)$ vacant territories (recall that $Nf\varphi_1\varphi_2 = N(1 - \psi)$ due to density-dependent factors, see Equation 2). Each of the newly recruited adults will produce f newborn offspring and provision them. Thus, 2 subpopulations can be identified in the population at time $t + 1$. Subpopulation A is composed of $N\psi$ broods, each of which is occupied by an adult who survived from the previous time unit with probability ψ. The numbers of age-1 and age-2 offspring in subpopulation A are $N\psi f$ and $Nf\varphi_1$, respectively. Subpopulation B is composed of $Nf\varphi_1\varphi_2$ broods, each of which is occupied by an adult who was an age-2 offspring in the previous time step. The number of age-1 offspring in subpopulation B is $Nf^2\varphi_1\varphi_2$, and there are no age-2 offspring in subpopulation B.

Because the population has already reached the evolutionary equilibrium at time t, the total number of age-2 offspring in the population at time $t + 1$ should remain at $Nf\varphi_1$, which is actually the number of age-2 offspring in subpopulation A. Likewise, the number of age-1 offspring in the entire population at time $t + 1$ should remain at Nf, which is the number of age-1 offspring in subpopulation A ($= N\psi f$) plus the number of age-1 offspring in subpopulation B ($= Nf^2\varphi_1\varphi_2 = Nf(1 - \psi)$). Consequently, each and every age-i ($i = 1, 2$) offspring in the entire population can be regarded as receiving x_i^* resources from its living parent at any given time step, with the average parental mortality holding constant at $1 - \psi$. The same can be said of a population with n offspring age classes.

C. Evolutionary stability and convergence stability

The second-order condition for the equilibrium point $(x_1^*, \ldots, x_n^*)$ to be ES is that the Hessian matrix of $\lambda(\mathbf{x}^\circ, \mathbf{x}^*)$ is negative semidefinite at that point (Day and Taylor 2003). In order to obtain the derivative of $\lambda(\mathbf{x}^\circ, \mathbf{x}^*)$ with respect to a mutant strategy $\mathbf{x}^\circ$, I use the following equation shown by Taylor and Frank (1996):

$$\left.\frac{\partial\lambda(\mathbf{x}^\circ, \mathbf{x}^*)}{\partial\mathbf{x}^\circ}\right|_{\mathbf{x}^\circ = \mathbf{x}^*} = \mathbf{v}^*\left(\left.\frac{\partial\mathbf{A}(\mathbf{x}^\circ, \mathbf{x}^*)}{\partial\mathbf{x}^\circ}\right|_{\mathbf{x}^\circ = \mathbf{x}^*}\right)\mathbf{u}^*/(\mathbf{v}^* \cdot \mathbf{u}^*), \tag{A3}$$

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 and A3, I obtain the $n \times 1$ vector of the derivative of $\lambda(\mathbf{x}^\circ, \mathbf{x}^*)$ with respect to a mutant strategy $\mathbf{x}^\circ$ and evaluate at $\mathbf{x}^\circ = \mathbf{x}^*$:

$$\left.\frac{\partial\lambda(\mathbf{x}^\circ, \mathbf{x}^*)}{\partial\mathbf{x}^\circ}\right|_{\mathbf{x}^\circ = \mathbf{x}^*} = \left[\left.\frac{\partial\lambda(\mathbf{x}^\circ, \mathbf{x}^*)}{\partial x_i^\circ}\right|_{x_i^\circ = x_i^*}\right]$$

$$= \left[\left.\frac{u_i v_{i+1}\varphi_i'(x_i) + u_p v_p u_i\psi'(E_x^\circ)}{n(1 - \psi(E_x^*)) + 1}\right|_{x_i^\circ = x_i^*}\right], \tag{A4}$$

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

$$\mathbf{M}_{ij} = \left.\frac{\partial^2 \lambda(\mathbf{x}^\circ, \mathbf{x}^*)}{\partial x_j^\circ \partial x_i^\circ}\right|_{\mathbf{x}^\circ = \mathbf{x}^*}. \tag{A5}$$

In order for $\mathbf{M}$ to be negative semidefinite at the equilibrium point $(x_1^*, \ldots, x_n^*)$, all its eigenvalues should be zero or negative. The Routh–Hurwitz condition for n-dimensional matrices can be used to determine the local stability of the $n \times n$ Hessian matrix $\mathbf{M}$. The actual calculation, however, is very cumbersome, and hence, the local maximum at the equilibrium point $(x_1^*, \ldots, x_n^*)$ was numerically verified.

Another stability criterion called convergence stability ensures evolutionary attainability through a series of small steps (Eshel and Motro 1981). Denote by $\hat{\mathbf{x}}(= \varepsilon\mathbf{x}^\circ + (1 - \varepsilon)\mathbf{x}^*)$ the mean of parental allocation strategies in a population with a rare mutant strategy $\mathbf{x}^\circ$ 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

$$\mathbf{J}_{ij} = \left.\frac{\partial}{\partial \hat{x}_j}\left(\left.\frac{\partial \lambda(\mathbf{x}^\circ, \mathbf{x}^*)}{\partial x_i^\circ}\right|_{\mathbf{x}^\circ = \hat{\mathbf{x}}}\right)\right|_{\hat{\mathbf{x}} = \mathbf{x}^*}, \tag{A6}$$

be a negative semidefinite at the equilibrium point $(x_1^*, \ldots, x_n^*)$ (Leimar 2005; Otto and Day 2007). The negative semidefiniteness of the matrix was numerically checked in the same manner as above.

D. The pattern of ES allocation when $\varphi_i'(x) > \varphi_{i+1}'(x)$ for all positive x

Equation 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}^*, I obtain the following:

$$\frac{\partial}{\partial x_{i+1}^*}\delta(x_{i+1}^*)$$
$$= \frac{\varphi_{i+1}(x_{i+1}^*)(\varphi_{i+1}''(x_{i+1}^*) - \varphi_i'(x_{i+1}^*)\varphi_{i+1}(x_{i+1}^*)) - (\varphi_{i+1}'(x_{i+1}^*))^2}{(\varphi_{i+1}(x_{i+1}^*))^2} < 0, \tag{A7}$$

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

Because 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 $\varphi_{i+1}'(x)$ approach zero as x approaches infinity, which implies that $\delta(x_{i+1}^*)$ approaches zero as x_{i+1}^* approaches infinity. Because $\delta(x_{i+1}^*)$ 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}^*.

E. 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 $\varphi_i'(x_{i+1}^*) < \varphi_{i+1}'(x_{i+1}^*)$, I can derive the following inequality:

$$\delta = \frac{\varphi_{i+1}'(x_{i+1}^*)}{\varphi_{i+1}(x_{i+1}^*)} - \varphi_i'(x_{i+1}^*) > \frac{\varphi_{i+1}'(x_{i+1}^*)}{\varphi_{i+1}(x_{i+1}^*)} - \frac{\varphi_i'(x_{i+1}^*)}{\varphi_i(x_{i+1}^*)} > 0. \tag{A8}$$

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:

$$\delta(\tilde{x}) = \frac{\varphi_{i+1}'(\tilde{x})}{\varphi_{i+1}(\tilde{x})} - \varphi_i'(\tilde{x}) = \frac{\varphi_{i+1}'(\tilde{x})}{\varphi_{i+1}(\tilde{x})} - \varphi_{i+1}'(\tilde{x}) > 0. \tag{A9}$$

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}^*.

REFERENCES

Bize P, Piault R, Moureau B, Heeb P. 2006. A UV signal of offspring condition mediates context-dependent parental favouritism. Proc R Soc Lond Ser B. 273:2063–2068.

Boland CRJ, Heinsohn R, Cockburn A. 1997. Experimental manipulation of brood reduction and parental care in cooperatively breeding white-winged choughs. J Anim Ecol. 66:683–691.

Charlesworth B. 1994. Evolution in age-structured populations. 2nd ed. Cambridge (UK): Cambridge University Press.

Charnov EL. 1993. Life history invariants: some explorations of symmetry in evolutionary ecology. Oxford: Oxford University Press.

Clutton-Brock TH. 1991. The evolution of parental care. Princeton (NJ): Princeton University Press.

Cotton PA, Wright J, Kacelnik A. 1999. Chick begging strategies in relation to brood hierarchies and hatching asynchrony. Am Nat. 153:412–420.

Day T, Taylor PD. 2003. Evolutionary dynamics and stability in discrete and continuous games. Evol Ecol Res. 5:605–613.

Eshel I, Motro A. 1981. Kin selection and strong evolutionary stability of mutual help. Theor Pop Biol. 19:420–433.

Fisher RA. 1930. The genetical theory of natural selection. Oxford: Oxford University Press.

Frank SA. 1998. Foundations of social evolution. Princeton (NJ): Princeton University Press.

Glassey B, Forbes S. 2002. Begging and asymmetric nestling competition. In: Wright J, Leonard ML, editors. The evolution of begging: competition, cooperation and communication. Dordrecht (The Netherlands): Kluwer Academic Publishers. p. 269–282.

Godfray HCJ. 1991. Signalling of need by offspring to their parents. Nature. 352:328–330.

Godfray HCJ. 1995. Signalling of need between parents and young: parent-offspring conflict and sibling rivalry. Am Nat. 146:1–24.

Haig D. 1990. Brood reduction and optimal parental investment when offspring differ in quality. Am Nat. 136:550–566.

Johnstone RA. 2004. Begging and sibling competition: how should offspring respond to their rivals? Am Nat. 163:388–406.

Kilner R. 1995. When do canary parents respond to nestling signals of need? Proc R Soc Lond Ser B. 260:343–348.

Kilner RM. 2002. Sex differences in canary (*Serinus canaria*) provisioning rules. Behav Ecol Sociobiol. 52:400–407.

Kilner RM, Johnstone RA. 1997. Begging the question: are offspring solicitation behaviors signals of need? Trends Ecol Evol. 12:11–15.

Krebs EA, Cunningham RB, Donnelly CF. 1999. Complex patterns of food allocation in asynchronously hatching broods of crimson rosellas. Anim Behav. 57:753–763.

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.

Leonard M, Horn A. 1996. Provisioning rules in tree swallows. Behav Ecol Sociobiol. 38:341–347.

Lessells CM. 2002. Parentally biased favouritism: why should parents specialize in caring for different offspring? Philos Trans R Soc Lond Ser B Biol Sci. 357:381–403.

Lloyd DG. 1985. Parallels between sexual strategies and other allocation strategies. Experientia. 41:1277–1285.

Lloyd DG. 1988. A general principle for the allocation of limited resources. Evol Ecol. 2:175–187.

Lotem A. 1998. Higher levels of begging behavior by small nestlings: a case of a negatively correlated handicap. Isr J Zool. 44:29–45.

Macnair MR, Parker GA. 1979. Models of parent-offspring conflict. III. Intra-brood conflict. Anim Behav. 26:111–122.

Magrath RD. 1990. Hatching asynchrony in altricial birds. Biol Rev. 65:587–622.

Metz JAJ, Nisbet RM, Geritz SAH. 1992. How should we define 'fitness' for general ecological scenarios? Trends Ecol Evol. 7:198–202.

Mock DW, Parker GA. 1997. The evolution of sibling rivalry. Oxford: Oxford University Press.

Mylius SD, Diekmann O. 1995. On evolutionarily stable life histories, optimization and the need to be specific about density dependence. Oikos. 74:218–224.

Otto S, Day T. 2007. A biologist's guide to mathematical modeling in ecology and evolution. Princeton (NJ): Princeton University Press.

Parker GA, Macnair MR. 1979. Models of parent-offspring conflict. IV. Suppression: evolutionary retaliation by the parent. Anim Behav. 27:1210–1235.

Parker GA, Mock DW, Lamey TC. 1989. How selfish should stronger sibs be? Am Nat. 133:846–868.

Parker GA, Royle NJ, Hartley IR. 2002. Begging scrambles with unequal chicks: interactions between need and competitive ability. Ecol Lett. 5:206–215.

Pen I, Weissing FJ. 2000. Towards a unified theory of cooperative breeding: the role of ecology and life history re-examined. Proc R Soc Lond Ser B. 267:2411–2418.

Pen I, Weissing FJ. 2002. Optimal sex allocation: steps towards a mechanistic theory. In: Hardy I, editor. Sex ratios: concepts and research methods. New York: Cambridge University Press. p. 26–45.

Price K, Harvey H, Ydenberg R. 1996. Begging tactics of nestling yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. Anim Behav. 51:421–435.

Price K, Ydenberg R. 1995. Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. Behav Ecol Sociobiol. 37:201–208.

Ricklefs RE. 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. Condor. 102: 9–22.

Rodríguez-Gironés MA, Cotton PA, Kacelnik A. 1996. The evolution of begging: signaling and sibling competition. Proc Natl Acad Sci USA. 93:14627–14641.

Royle NJ, Hartley IR, Parker GA. 2002. Begging for control: when are offspring solicitation behaviors honest? Trends Ecol Evol. 17:434–440.

Rubenstein DI. 1982. Reproductive value and behavioral strategies: coming of age in monkeys and horses. Perspect Ethol. 5:469–487.

Sargent RC, Gross MR. 1986. William's principle: an explanation of parental care in teleost fishes. In: Pitcher T, editor. The behavior of teleost fishes. London: Croom Helm Publishers. p. 275–293.

Smiseth PT, Amundsen T. 2002. Senior and junior nestlings in asynchronous bluethroat broods differ in their effectiveness of begging. Evol Ecol Res. 4:1177–1189.

Smiseth PT, Bu RJ, Erikenaes AK, Amundsen T. 2003. Food limitation in asynchronous bluethroat broods: effects on food distribution, nestling begging, and parental provisioning rules. Behav Ecol. 14:793–801.

Smith CC, Fretwell SD. 1974. The optimal balance between size and number of offspring. Am Nat. 108:499–506.

Stamps J, Clark A, Arrowood P, Kus B. 1985. Parent-offspring conflict in budgerigars. Behaviour. 94:1–40.

Taylor PD. 1990. Allele frequency change in a class-structured population. Am Nat. 135:95–106.

Taylor PD, Frank SA. 1996. How to make a kin selection model. J Theor Biol. 180:27–37.

Temme DH. 1986. Seed size variability: a consequence of variable genetic quality among offspring? Evolution. 40:414–417.

Trivers R. 1974. Parent-offspring conflict. Am Zool. 14:249–264.

West-Eberhard MJ. 1975. The evolution of social behavior by kin selection. Q Rev Biol. 50:1–33.

Winkler DW. 1987. A general model for parental care. Am Nat. 130:526–543.