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Within-Brood Competition and the Optimal Partitioning of Parental Investment

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ABSTRACT: In this article, we introduce a simple within-brood competitive growth model that maximizes parental fitness in unpredictable food conditions in species that exhibit parental care, progressive provisioning, and an initial brood overproduction. We argue that competition between siblings may provide a proximate mechanism for parents to adjust the number of surviving offspring or the social organization of the group in social species to food conditions.

Keywords: growth, parental investment, sibling competition, fitness.

How limited resources should be divided among offspring is a problem that, in many cases where there is parental care, parents have to solve. Smith and Fretwell (1974) have shown with a simple model—where parental investment is represented as a single quantity, offspring's fitness is a direct function of the amount of investment received, offspring are identical in quality, and parental fitness is defined as the return in offspring fitness by unit of investment—that parents should invest the same amount in each offspring. Smith and Fretwell's (1974) graphic model has been formalized by Lloyd (1987) and extended by several authors (Brockelman 1975; Temme 1986; McGinley and Charnov 1988; Haig 1990). But, in

the case of a brood comprising several initially identical or almost identical offspring, when resources such as food are too limited to raise all offspring, such models predict that an equal amount of investment should be allocated to each offspring, while a more appropriate solution would be to allocate more investment to some (possibly arbitrarily selected) offspring while not investing in others: in this way, at least those offspring that receive enough investment can reach maturity and eventually reproduce. Another solution, which avoids the problem of brood reduction, is to produce the number of young or eggs that maximizes expected offspring fitness (Brockelman 1975): offspring production may be naturally reduced in response to poor food conditions because, for example, producing a young or an egg requires a certain level of resources. Even if offspring production is not costly, available resources may conceivably regulate reproductive activity. But it may also happen, especially when the production of young or eggs is not a limiting factor, that a larger brood is produced than can actually be raised. Cases where a surplus progeny is produced are reviewed in Mock and Forbes (1995). Initial overproduction by parents, a widespread feature across many "nursery" taxa (Mock and Parker 1997), is usually explained by three categories of mutually compatible hypotheses (Mock and Forbes 1995; Mock and Parker 1997).

The first category is the "resource-tracking" hypothesis (Temme and Charnov 1987). Parents create an "optimistic" number of offspring to capitalize on unpredictably favorable years. This hypothesis implies that parents have incomplete information about forthcoming resources, an idea already incorporated in Lack's (1947, 1954) original argument about the adaptive value of brood reduction (see also Temme and Charnov 1987; Forbes and Ydenberg 1992; Pijanowski 1992; Forbes 1993; Konarzewski 1993; Forbes and Mock 1996).

Second is the "offspring facilitation" hypothesis. Some offspring may end up helping their siblings to survive and/or reproduce. This includes a wide spectrum of different phenomena, from sibling cannibalism to helpers in social species.

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Third, there is the "replacement offspring" hypothesis, "insurance" hypothesis, or "progeny choice" hypothesis, which are three variations on a single idea—that surplus progeny can be used to replace offspring that are either not viable or die.

When there is an overproduction of offspring, differential parental investment, leading to the possible elimination of some of the offspring or to a differentiation of offspring into reproducers and helpers, is necessary to maximize parental fitness. Such differential investment may involve quite complex decisions and the evaluation of the state of each offspring. The aim of this article is to show, with a simple competitive growth model based on a single resource and a nonlinear weight-fitness relationship, that an appropriate level of "competition" among offspring can offer a solution to the problem of differential parental investment. The term *competition* is not to be taken too narrowly: it includes lethal or nonlethal, direct or indirect, aggressive or nonaggressive, fight-based or scramble-based forms of competition (see Mock and Parker 1997 for a taxonomy of sibling rivalry).

It has been noted by several researchers (Uchmanski 1985; Kimmel 1986; Lonnicki 1988) that competition implies skewness: for example, competition for food leads to weight differentiation if there is a positive feedback mechanism such that larger or heavier individuals are more likely to get more food. This is very simple to understand: the more food an individual gets, the more food it is likely to get, so that, under conditions of limited resources, there is less food left for other individuals, some of whom may rapidly die through a similar, but inverted, amplification mechanism. If, on the other hand, resources are plentiful, competition may not lead to skewness because all individuals receive all the resources they need, assuming that parents are willing to invest as much as the young ask for. The rest of this article is dedicated to developing a simple mathematical formalism for this verbal argument. The deterministic growth model used in this article is in many respects similar to the one introduced by Uchmanski (1985), who also provides an extensive list of empirical observations of weight distributions. Another related model, in a different context, is Nijhout and Wheeler's (1996) model of the competitive growth of imaginal structures in holometabolous insects, which produces complex allometries.

Parental Fitness

Let us assume that the direct fitness S (scaled between 0 and 1) of an individual depends on its weight w at maturity as

$$S(w) = \frac{w^n}{w^n + \theta^n}, \quad (1)$$

where θ is a threshold and n a parameter describing the steepness of $S(w)$ at the threshold. Fitness certainly depends on other factors than weight, but we focus for simplicity on this sole aspect in the present article. Figure 1 shows $S(w)$ curves for several values of n and $\theta = 1$. This type of sigmoid-shaped weight-fitness (or investment-fitness) relationship has been used and discussed by numerous authors (e.g., Smith and Fretwell 1974; Brockelman 1975; Lloyd 1987; Parker et al. 1989; Nonacs 1993). The variable $S(w)$, given by equation (1), exhibits increasing returns for $w < \theta(n - 1/n + 1)^{1/n} \equiv \theta_c$, and decreasing returns for $w > \theta_c$; θ_c is the value at which returns are maximal. Most previous authors have been concerned with the region $w > \theta_c$, where there are diminishing returns.

We assume for simplicity that parental fitness, S_p , is the sum of all individual offspring fitnesses and not the return in this quantity per unit of investment:

$$S_p = \sum_{i=1}^N [w_i^n / (w_i^n + \theta^n)], \quad (2)$$

where N is the number of offspring and w_i the weight of individual i . Only the current brood is taken into account to compute parental fitness; obviously, a more complete model should sum over all broods produced in the parents' lifetime and include the effects of investing in the current brood on future broods. We take equation (2) as an approximation. Given the definition of S_p , what is the parent(s)' optimal brood weight distribution? If one neglects growth dynamics as a first approximation, one can assume that there is a total amount of weight W to be shared by the brood. The question is then equivalent to, How should W be partitioned among offspring to maximize parental fitness? Because there are increasing returns up to $w_i = \theta_c$, the optimal parental strategy is to raise as many young as possible to $w_i = \theta_c$, leaving the other young at $w \approx 0$. To understand this, imagine that the steepness of S is infinite ($n = \infty$): $S = 0$ for $w < \theta_c = \theta$, and $S = 1$ for $w > \theta_c$. When $W < N\theta_c$ parental fitness is maximized by allocating weight to m individuals such that $m\theta_c \leq W < (m + 1)\theta_c$. When $W \geq N\theta_c$, there should be an even partitioning of resources among offspring, each offspring reaching a weight $w = W/N$.

It is clear at this point that the number of offspring that should be raised to maturity depends on W , the amount of resources available. An important question is, therefore, How do parents allocate food to maximize their fitness in response to food availability, if they do not know W in advance? Our suggestion is that a possible answer lies in within-brood competition, which can take many forms. In what follows, we assume that competition plays a role only in how available resources are

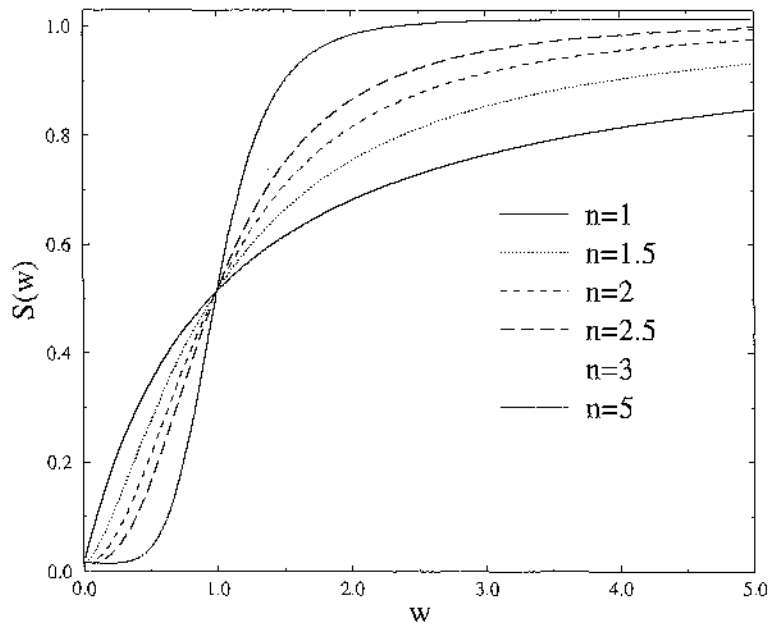


Figure 1: Fitness function $S(w) = w^n/(w^n + \theta^n)$, where $\theta = 1$ is a threshold and $n = 1, 1.5, 2, 2.5, 3, 5$ is a parameter describing the steepness of $S(w)$ at the threshold.

shared. We do not make any assumption about how larger individuals have access to more food than smaller ones, we simply assume that they do. It may be that they beg more easily (more loudly, more frequently, or by emitting more pheromone), prevent their siblings from accessing food, or have a more active metabolism, and so forth. Assuming a particular form of competition would certainly influence the detail of the model but not its fundamental properties. Where competition relies on begging, our model indicates that begging can be “honest” because only fit individuals can afford to beg loudly (Zahavi and Zahavi 1997) and not, as usually is the case in models of offspring signaling (Godfray 1995a, 1995b), because it reflects an individual’s poor condition. Most interesting begging models assume that parents cannot evaluate the condition of their offspring and have to rely on signals emitted by the offspring. Offspring condition may not, however, be cryptic: for example, it is difficult for a small larva to look large or, in the context of avian sibling rivalry, a difference should be clearly made between begging signals and physical dominance whereby an individual blocks the entrance of the nest and is the first to have access to food. We consider here only the case where offspring condition is not cryptic.

Competitive Growth Model

Let us assume a constant flow Φ per unit time of food into the nest: parents are progressive provisioners that

supply offspring repeatedly with food throughout the developmental period. This situation is the most common when there is parental care, either in insects or in birds and mammals. Although assuming a constant Φ may seem to reduce the scope of the model, the other underlying assumption is that Φ is unknown to the parents at the time offspring are produced and raised. A more realistic model would include a variable Φ . The dynamics of Q , the quantity of food available for consumption by the brood, is given by

$$\partial_t Q = \Phi - \sum_{i=1}^N Q_i, \quad (3)$$

where Q_i is the amount consumed by individual i per unit time, and ∂_t denotes the time derivative. A critical assumption here is that Q_i depends on the amount of food available, Q , and on a level of food consumption, βw_i^p , where $p \geq 0$ is a parameter that determines the level of competition between siblings (the function of p will become clearer below):

$$Q_i = \frac{\beta w_i^p Q}{C + Q}, \quad (4)$$

where C is a threshold. When food is abundant, which is defined by $Q \gg C$ (the amount of food available is significantly greater than the threshold C), Q_i tends to βw_i^p . The amount of food that an individual of weight w_i would ideally consume per unit time is, therefore, repre-

sented by βw_i^p . We assume that the (prematurity) growth equation of individual i is given by the logistic equation

$$\partial_t w_i = \alpha Q_i \left(1 - \frac{w_i}{w_m} \right) - \gamma w_i, \quad (5)$$

where α is a metabolic parameter, w_m is the maximum weight that can be reached by an individual and γ the rate of weight loss. The choice of the logistic growth equation is arbitrary; we have checked that other widely used growth equations (Gompertz and Von Bertalanffy equations) yield qualitatively similar results. If we assume that the dynamics of Q , the total amount of food available for the brood, occurs on a faster timescale than the dynamics of w (quite a reasonable assumption: animals usually gain weight more slowly than food flows in), we can consider that Q quickly reaches its stationary value for a given set of values $\{w_i\}$:

$$Q = \frac{\Phi C}{\beta \sum_{i=1}^N w_i^p - \Phi}. \quad (6)$$

The denominator of equation (6) should not become ≤ 0 . Let us emphasize that relaxing the timescale separation assumption makes the mathematics less tractable and more difficult to understand but does not alter the model's properties: direct numerical integration of equations (4)–(5) without assuming the faster dynamics of Q leads to essentially the same results.

After some simple algebra, the dynamics of w_i is then given by

$$\partial_t w_i = \alpha \Phi \frac{w_i^p}{\sum_{j=1}^N w_j^p} \left(1 - \frac{w_i}{w_m} \right) - \gamma w_i. \quad (7)$$

In equation (7), the term $w_i^p / \sum_{j=1}^N w_j^p$ indicates explicitly that there is competition among offspring, the level of which is parameterized by p : the larger w_i the larger the share of individual i , reflected in the growth coefficient $\alpha \Phi w_i^p / \sum_{j=1}^N w_j^p$. More precisely, the share of individual i is larger if w_i is larger than the weights of other individuals. Egalitarian food allocation is obtained when $p = 0$, which amounts to replacing the expression of Q_i in equation (4) by $Q_i = \Phi/N$, for all i (i.e., all individuals receive Φ/N per unit time). Competition increases with p : when p becomes infinite, the largest individuals have access to all the food. The p parameter, the value of which is assumed to be identical for all individuals, is an important parameter since a sufficient level of competition is required to allow for differentiation when food is scarce,

but too much competition is not appropriate when food is abundant.

For the analysis that follows, we assume that development time is sufficient for stationary states to be reached; it may not always be the case, but even when development time is shorter than the time required to reach stationarity (a regime in which w does no longer vary significantly), there may already be some, possibly incomplete, differentiation among offspring. Ideally, development time should be taken into account in a more realistic model.

Results

Let us first examine the stationary state of equation (7), defined by $\partial_t w_i = 0$, when $p = 1$. In the stationary state, the weight w_i of individual i is given by

$$w_i = 0 \quad (8a)$$

or

$$w_i = w_s \equiv \alpha \Phi w_m / (\alpha \Phi + \gamma n_s w_m), \quad (8b)$$

where n_s is the number of offspring that survive (defined here by $w_i \neq 0$). All surviving offspring have the same final weight w_s in this model, but w_s depends on how many actually survive: w_s decreases as n_s increases. This result can be generalized to other values of p , although no simple analytical expression is available for w_s .

For all values of p , numerical integration of this deterministic model indicates that the number of surviving offspring n_s is a function of the competition parameter p , the inflow of food per unit time Φ , the growth parameter α , the rate of weight loss γ , the maximum possible weight w_m , and the variance σ^2 of the initial weight distribution $\{w_i(t=0)\}_{i=1, \dots, N}$ which is taken to be Gaussian with mean $\langle w \rangle_{t=0}$. The larger σ^2 , the smaller the number of surviving offspring n_s , an expected result as larger initial weight differences imply biased food allocation from the start. Intrinsic differences in weights at emergence or a hatching asynchrony may be reflected in σ^2 . Although, strictly speaking, our model cannot generate differentiation if $\sigma^2 = 0$ (no initial weight differentiation) because it is a deterministic model, any stochasticity (fluctuations) in the growth or food allocation processes will have the same effect as having $\sigma^2 \neq 0$, and fluctuations are highly unlikely not to occur. Moreover, however small σ^2 , initial weight differences are amplified in the model if food is scarce. Therefore, assuming that there are initial weight differences between offspring is not a limitation.

If one assumes that the growth parameter α , the rate of weight loss γ , the maximum weight w_m , and the initial variance σ^2 are fixed, which is a reasonable approxima-

tion if these parameters fluctuate around well-defined values characteristic of the considered species, the number of surviving offspring n_s is a function of the competition parameter p and the inflow of food per unit time Φ , as is the weight of surviving offspring w_s , which can be written $w_s(n_s(p, \Phi), p, \Phi)$. The parental optimal value $\hat{n}_s(\Phi)$ of n_s for a given value of Φ is approximately defined by $w_s(\hat{n}_s(\Phi)) \equiv \hat{w}_s(\Phi) \geq \theta_e$ and $w_s[\hat{n}_s(\Phi) + 1] < \theta_e$, where θ_e is the peak of the marginal returns of the fitness function given in equation (1). Again, the argument is simple: the parents should raise as many offspring as possible to $w = \theta_e$. If all individuals can reach a weight greater than θ_e , then, when Φ is sufficiently large $\hat{n}_s = N$. In the absence of competition ($p = 0$), that is, when Q_i , the amount of food consumed per unit time by individual i , is replaced in equation (4) by $Q_i = \Phi/N$, we have $n_s = N$ and the corresponding weight w_e reached by all individuals is equal to the weight w_s one would obtain with competition ($p \neq 0$) for $n_s = N$: that is, $w_e = w_s(n_s = N, p, \Phi)$. This means that $p = 0$ can be optimal only when resources are abundant because it leads to full survivorship. Let Φ_s be the value of Φ such that full survivorship should be favored for $\Phi > \Phi_s$. Biased allocation of resources is required when $\Phi < \Phi_s$ but is not necessary when $\Phi > \Phi_s$.

Is there, however, a value p_0 of p such that $n_s(p_0, \Phi) = \hat{n}_s(\Phi)$ for any value of Φ ? In particular, p_0 should satisfy $n_s(p_0, \Phi > \Phi_s) = N$: when resources are abundant, all offspring should survive. Such a value of p , if it ex-

isted, would automatically implement the parental optimal through offspring competition. Numerical integration of the growth equations suggests that such a value of p exists. Figure 2 shows the stationary weight of stationary offspring as a function of Φ , $w_s(\Phi)$, for four different values of the competition parameter p (0, 1.2, 1.4, and 1.8) with $\alpha = 1$, $\gamma = 0.03$, $w_m = 3$, $\sigma^2 = 0.05$, $\langle w \rangle_{t=0} = 0.1$, $N = 20$, $n = 5$, $\theta = 1$. For these values of the parameters, $\theta_e = 0.922$. When $p = 0$, $w_s = \alpha\Phi w_m / (\alpha\Phi + \gamma N w_m)$, which becomes equal to θ_e at $\Phi_s = \gamma N w_m \theta_e / [\alpha(w_m - \theta_e)]$ (here, $\Phi_s \approx 0.8$). When $p = 1.4$, w_s is very close to $\hat{w}_s = \theta_e$ until it meets the $p = 0$ curve exactly at $\Phi = \Phi_s$; $p = 1.4$ seems to represent an ideal level of competition. When $p = 1.2$, w_s lies significantly below θ_e when Φ is small: there are too many survivors, none of which has a sufficient weight. When $p = 1.8$, the opposite phenomenon takes place: a few individuals have a large weight and a correspondingly large fitness, but the fitness gained by these individuals by growing large is smaller than the loss in parental fitness due to the death of other offspring. Figure 3 shows the number of surviving offspring as a function of Φ , $n_s(\Phi)$. When $p = 1.2$, n_s converges too quickly to N ; there are too many survivors between $\Phi = 0$ and $\Phi = \Phi_s$. When $p = 1.8$, on the other hand, n_s is too small over the whole range of Φ values. When $p = 1.4$, n_s is intermediate. Let us recall that when $p = 0$, $n_s(\Phi) = N$ for all Φ . Figure 4 shows the parental fitness $S_p(\Phi)$. When $p = 0$, $S_p(\Phi) = N[w_s^2 / (w_s^2 + \theta^2)]$, where $w_s = \alpha\Phi w_m / (\alpha\Phi + \gamma N w_m)$ (see eq. [8.1]). When

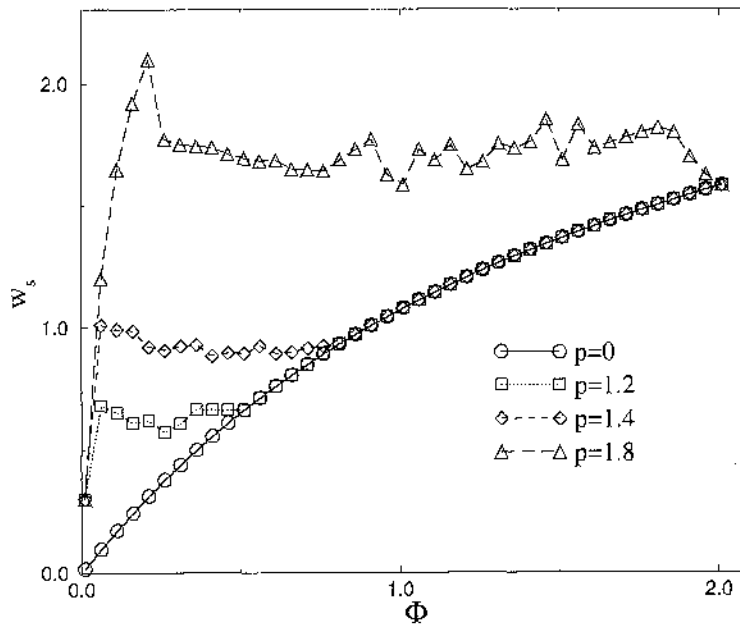


Figure 2: Stationary weight $w_s(\Phi)$ of surviving individuals for four different values of p (0, 1.2, 1.4, 1.8) with $\alpha = 1$, $\gamma = 0.03$, $w_m = 3$, $\sigma^2 = 0.05$, $\langle w \rangle = 0.1$, $N = 20$, $n = 5$, $\theta = 1$ ($\theta_e = 0.922$).

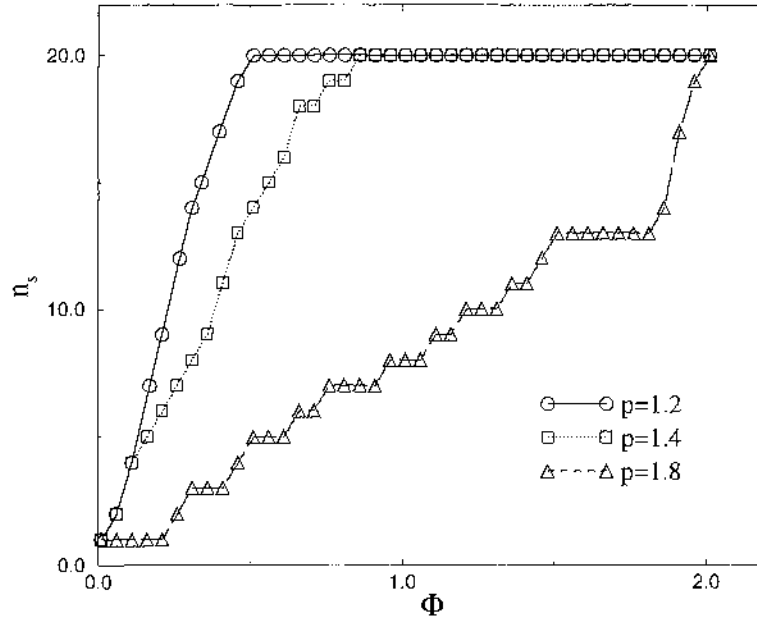


Figure 3: Number of surviving individuals $n_s(\Phi)$ for three different values of p (1.2, 1.4, 1.8) with the same values of the parameters as in figure 2. For $p = 0$ (no competition), $n_s(\Phi) = 0$ for all Φ .

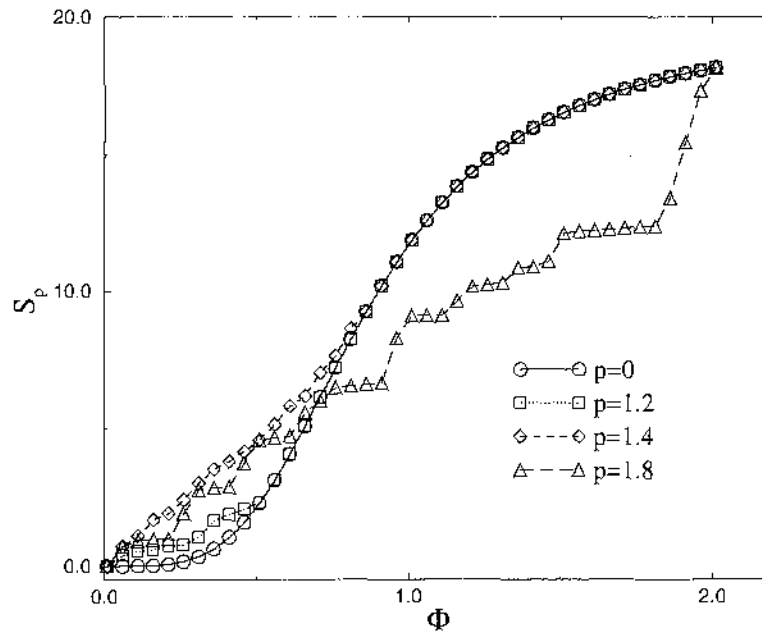


Figure 4: Parental fitness $S_p(\Phi)$ for four different values of p (0, 1.2, 1.4, 1.8) with the same values of the parameters as in figure 2.

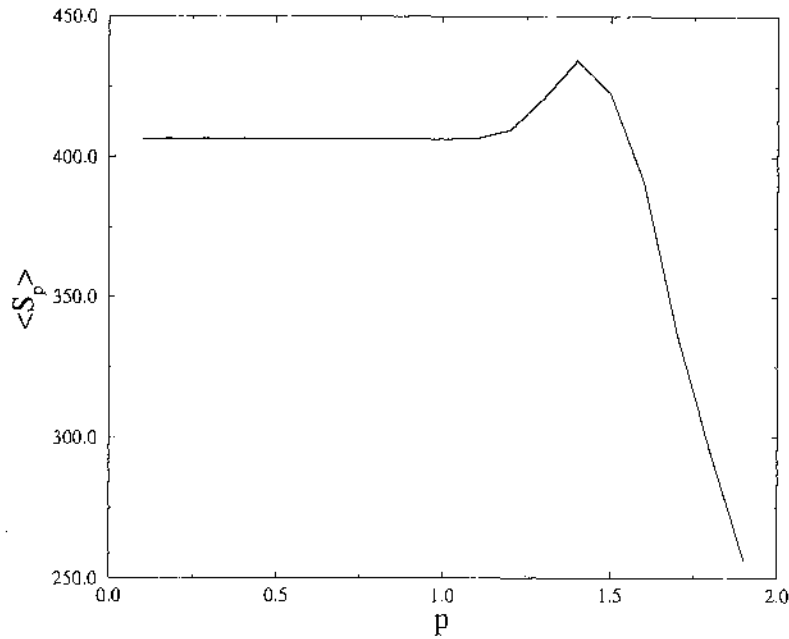


Figure 5: Parental fitness $\langle S_p(p) \rangle$ averaged over $\Pi(\Phi)$, where $\Pi(\Phi)$ is a uniform distribution in the interval $[0, \Phi_m]$, where Φ_m is the maximum possible rate of food inflow, with the same values of the parameters as in figure 2.

$p = 1.2$, $S_p(\Phi)$ reaches the $p = 0$ curve too early. When $p = 1.8$, $S_p(\Phi)$ lies above the $p = 0$ curve for $\Phi < 0.7$ but then lies below the $p = 0$ curve. When $p = 1.4$, the curve never lies below the $p = 0$ curve because the $p = 1.4$ strategy combines biased allocation when food is scarce with even allocation when food is abundant. Therefore, a single value $p_0 = 1.4$ of p , the level of competition, allows the parental optimal to be reached for all values of Φ .

In order to more explicitly include the fact that the value of Φ is unknown to the parents, let us now assume that Φ is a random variable with probability density $\Pi(\Phi)$, the realization of which is fixed over the time it takes to raise the offspring. The average parental fitness $\langle S_p(p) \rangle$ over $\Pi(\Phi)$ for a given value of the competition parameter p is given by

$$\langle S_p(p) \rangle = \int_{\Phi=0}^{\Phi=\infty} \Pi(\Phi) \bar{n}_s(p, \Phi) S(\bar{w}_s(p, \Phi)) d\Phi, \quad (9)$$

where $\bar{n}_s(p, \Phi)$ and $\bar{w}_s(p, \Phi)$ are, respectively, the average number of surviving offspring and the average stationary weight reached by these surviving offspring at given p and Φ ($\bar{n}_s(p, \Phi)$ and $\bar{w}_s(p, \Phi)$ depend on the initial weight distribution). For the numerical integration, we assume that $\Pi(\Phi)d\Phi = d\Phi/\Phi_m$, that is, Φ is uniformly distributed in the interval $[0, \Phi_m]$, where Φ_m is the maximum possible rate of food inflow. Figure 5 shows $\langle S_p(p) \rangle$ as a function of p : there is clear maximum at $p = 1.4$. Note that $\langle S_p(p) \rangle$ decreases quickly when

competition becomes more intense: this is because the cost of competition becomes large as food becomes abundant.

Limitations of the Model

Our model deals with the case of brood reduction by elimination of some offspring, which is quite a radical method. Although it does convey the essence of our argument in its present form, the model can be refined to allow for more complicated stationary weight distributions than the bimodal distribution (dead or alive) described in this article. In social insects, for example, where it is possible for an individual to have a significant fitness without being large and without being able to reproduce, discrete or continuous caste distributions, rather than simply weight distributions, could be determined by a competitive growth process (Wheeler 1986).

The model can certainly be made more realistic by resorting to a stochastic description of the competitive growth process (Uchmanski 1985): this would allow one to avoid the assumption of an initial variance in the weight distribution. Also, we assumed that development time was not a limiting factor, which is obviously not always true: development time is a life-history trait that should be taken into account. More generally, our growth model is a crude approximation. More complex models can also include more than a single component

of fitness (here, body weight), more than one kind of resource (McGinley and Charnov 1988), and other types of competitive interactions among offspring.

Finally, we have made two assumptions—that the competition parameter p was identical for all offspring and that p did not vary as a function of food availability. The first assumption raises an issue because it may be that competitive growth is not evolutionarily stable: Why could the optimal value of p not be invaded by higher values of p ? We have several partial answers to offer to this question. First, food allocation may be mediated by the parents or workers, who distribute food on the basis of a noncryptic condition: then, p may not be a property of the offspring but a property of the parents, and it is in the advantage of the parents to adjust the value of p to its optimum. Second, even if the competition parameter p is a property of offspring, those offspring with a high value of p will have offspring with high values of p : the gain made early in life by this individual by growing larger than its siblings may be more than offset by its loss in fitness as a parent, especially in view of figure 5, which shows that the loss in parental fitness is dramatic when p exceeds its (parental) optimum. Finally, epistatic interactions among genes may prevent p from growing large if this leads to a reduction in inclusive fitness. These are, however, only partial answers, and a more careful study of the model with respect to this issue should be undertaken.

The second assumption is interesting to discuss: according to Lack (1966, p. 309), “a well-fed chick does not attack its nest-mate,” suggesting that, in the context of our model, the competition parameter p should be a decreasing function of the flow of food per unit time Φ . But, as noted by Mock and Parker (1997, p. 124), Lack’s (1966) statement has been widely accepted, and “dignified with a label, the food amount hypothesis,” without much empirical support. Many attempts to prove this hypothesis remain inconclusive. Mock et al. (1987) report that there is a very weak positive correlation between flight rate and food abundance in great egrets and blue herons. This supports the idea that the level of competition does not depend on food availability, as has been assumed in this article.

Discussion

In conclusion, we have shown, with a highly simplified model of growth and competition, how competition can lead to the parental optimal partitioning of resources among offspring. We believe that this model is applicable to a wide range of cases where the brood is provisioned progressively by parents (or workers in social insects),

when a larger brood is initially produced than can be raised successfully to a reproductive state.

This model of competition-based food allocation is consistent with, and provides a proximate mechanism for, the resource-tracking, offspring facilitation, and progeny choice/insurance hypotheses. It explicitly deals with the problem of incomplete information involved in the resource-tracking hypothesis. If one assumes that individuals differentiate into reproductives or helpers (instead of alive and dead), the model provides a new approach to social differentiation in the context of the offspring facilitation hypothesis: for example, in social insects, the fate of a larva (e.g., worker or reproductive) is often determined by its diet (Wheeler 1986). The amount and quality of resources available may determine whether, and to what extent, these resources will be allocated to the production of gynes versus workers. A general trend that has been observed in several ant species (Crozier and Pamilo 1996) is that the costly production of gynes is greatly reduced during years when food is scarce, leading to male-biased sex ratios and the production of workers; when food is abundant, many more gynes and fewer workers are produced: the adjustment of sex ratios to food conditions could be explained, at the proximate level, by a competition-based model such as the one presented in this article.

The progeny choice/insurance hypothesis may also be considered in the perspective of this model. Let us assume that one fit individual dies during its growth: more food will be available for others, and because the competitive growth model automatically regulates the number of surviving offspring, another individual (most probably an individual with an already relatively large weight) will replace its dead sibling. Let us also assume that a given individual is less fit than average, a feature that is reflected, for example, in that individual’s initial growth factor or weight. The competitive growth model is likely to lead to the elimination of that individual. The same outcome would result from the parents being able to detect the offspring’s lower quality and investing less in that offspring (Haig 1990).

A single model, the “competitive growth” model, therefore provides a potential proximate mechanism that combines all the possible parental payoffs for initial brood overproduction. Despite the model’s limitations, we believe that the conclusion reached—that competition between siblings may provide a proximate mechanism to maximize parental fitness in an uncertain environment—is quite robust. An additional weakness of the model is the current lack of experimental evidence that could provide us with values for the parameters used in this article. However, this model is a starting point for

new experiments aimed at determining its scope and relevance.

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