



Siblicide: The Evolutionary Blackmail

Miguel A. Rodriguez-Girones

The American Naturalist, Vol. 148, No. 1 (Jul., 1996), 101-122.

Stable URL:

<http://links.jstor.org/sici?sici=0003-0147%28199607%29148%3A1%3C101%3ASTEB%3E2.0.CO%3B2-L>

The American Naturalist is currently published by The University of Chicago Press.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ucpress.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

SIBLICIDE: THE EVOLUTIONARY BLACKMAIL

MIGUEL A. RODRÍGUEZ-GIRONÉS*

Department of Zoology, South Parks Road, Oxford OX1 3PS, United Kingdom

Submitted March 16, 1995; Revised August 21, 1995; Accepted October 11, 1995

Abstract.—Avian siblicide, whereby some chicks are eliminated from a brood as a direct consequence of sibling aggression, has often been interpreted as the outcome of a parent-offspring conflict over brood size. This conflict, which arises from the fact that each offspring values itself more than it values its siblings, results in offspring favoring smaller families, of higher-quality individuals, than would be optimal for their parents to produce. Considered as an evolutionary game, this conflict is complicated by two factors: before deciding to enforce their preferred brood size by eliminating unwanted brood mates, offspring must take into account the readjustments in parental investment that will normally ensue from brood reduction. Likewise, optimal parental investment will depend on offspring reaction to it. In particular, it is shown that the cost that parents must pay to provide enough resources to prevent siblicide will often be smaller than the benefit they obtain from maintaining their preferred brood size. Siblicide can be viewed in these instances as evolutionary blackmail, because its threat is sufficient to make parents increase brood provisioning levels. As a result of the blackmail, sibling aggression may acquire a signaling role in the parent-offspring interplay.

Avian brood reduction is a common phenomenon and has been thoroughly studied both at the theoretical and experimental levels (Lack 1947; O'Connor 1978; Drummond 1987; Parker and Mock 1987; Godfray and Harper 1990; Mock et al. 1990). It is normally the result of sibling competition—often the outcome of begging competitions (Ricklefs 1965; Magrath 1989; Lamey and Mock 1991) and sometimes the result of physical contests in which smaller or weaker chicks are killed by their siblings or die after being expelled from their nests (Drummond 1987; Mock et al. 1990; Mock and Forbes 1992). Theoreticians have focused mainly on the potential conflict of interest between parents and their surviving offspring that underlies siblicide. First-generation models (O'Connor 1978; Godfray and Harper 1990) predicted that a genetic parent-offspring conflict (POC) should underlie brood reduction. There is, however, little or no behavioral evidence of such conflict (Drummond et al. 1986). One of the models' assumptions that could be systematically violated is that parental investment (PI) in the entire brood does not change after brood reduction (Mock and Lamey 1991; B. J. Ploger, unpublished manuscript; M. A. Rodríguez-Gironés and H. Drummond, unpublished data). As pointed out by Forbes (1993), parents should adjust their level of investment to current brood size, hence reducing investment in a brood after siblicide has occurred. Forbes's game theoretical model shows that taking into account the adjustment in pa-

* Present address: Department of Zoology, Tel-Aviv University, 69978 Ramat-Aviv, Israel.

rental investment could greatly modify the picture presented by first-generation models. The logic of his argument is faultless. As I will show below, however, it needs to be extended one step further in order to find the evolutionarily stable strategy (ESS) of the game. Besides, I find the development of Forbes's model and conclusions drawn from it somewhat controversial.

In this article I will first present the results of a numerical analysis of Forbes's model. This I will do for two main reasons. First, there are a number of algebraic errors or typos in the original article that some readers may not detect. For this reason, I will give the main steps followed in the numerical analysis. (Intermediate calculations needed to derive the final results will not be presented; the reader will find the logic of these steps clearly explained in Forbes's original article.) Second, I would like to present the results of the numerical simulations from a slightly different point of view. After presenting the model, I will show how it can be extended to find the ESS and discuss the results.

STARTING POINT AND FIRST MOVE

Algebraic Solution

Siblicide will be considered a sequential game between parents and their offspring. Parents choose a clutch size and a level of investment. Chicks can choose to commit siblicide, and parents may readjust their level of investment to the new brood size. Following Forbes (1993), I will use the following notation and functional forms: B denotes brood size, B^* is the brood size favored by the parents in the absence of sibling aggression, M is the level of parental investment in the entire brood, assumed to have an absolute maximum value M_H ($0 \leq M \leq M_H$). A parent investing M units of PI in its current brood can expect a future reproductive success $f(M)$ given by

$$f(M) = \begin{cases} f_H & \text{if } M \leq 0 \\ f_H \left[1 - \left(\frac{M}{M_H} \right)^\theta \right] & \text{if } 0 < M < M_H \\ 0 & \text{if } M_H \leq M, \end{cases} \quad (1)$$

where f_H is the parents' expected future reproductive success if it makes no reproductive attempt during the current season and the parameter θ determines the relationship between parental investment and the cost of reproduction. Equation (1) indicates that future expected reproductive success decreases as investment in the present brood, M , increases, and it becomes negligible if the adult tries to exceed the maximum level M_H (the adult dies or is seriously handicapped). The probability $\rho(m)$ that a chick joins the breeding population after receiving m units of PI is

$$\rho(m) = \begin{cases} 1 - \frac{m_v}{m} & \text{if } m > m_v \\ 0 & \text{if } m \leq m_v. \end{cases} \quad (2)$$

TABLE 1
 PROPORTION OF PARENTAL RESOURCES CONSUMED BY THE μ -TH CHICK IN A B -CHICK BROOD UNDER
 DESPOTIC ALLOCATION, $P_{B,\mu}$

	$B = 1$	$B = 2$	$B = 3$	$B = 4$	$B = 5$	$B = 6$	$B = 7$	$B = 8$	$B = 9$	$B = 10$	$B = 11$	$B = 12$
$\mu = 1$	1.00	.59	.41	.315	.255	.215	.185	.163	.145	.131	.119	.110
$\mu = 2$.41	.35	.281	.234	.201	.175	.155	.139	.126	.115	.106
$\mu = 3$.24	.240	.209	.184	.163	.147	.133	.121	.111	.102
$\mu = 4$.164	.179	.164	.150	.137	.125	.115	.107	.099
$\mu = 5$.122	.140	.134	.126	.117	.109	.101	.095
$\mu = 6$.096	.114	.112	.107	.102	.096	.090
$\mu = 7$.078	.096	.096	.093	.090	.085
$\mu = 8$.066	.082	.083	.082	.080
$\mu = 9$.056	.071	.073	.073
$\mu = 10$.049	.063	.065
$\mu = 11$.043	.056
$\mu = 12$.038

There is a minimum level of resources m_v below which chicks are not viable, and above that minimum level viability increases hyperbolically with the amount of resources obtained. Forbes considers two possible scenarios: equal allocation of resources among chicks, in which each chick in the brood receives $m = M/B$ units of PI, and despotic allocation, in which there is a strict nestling hierarchy. With despotic allocation of resources, the dominant chick (α) decides what share of the parentally provided resources it will consume; the second-dominant chick (β) decides what share of the resources left by its dominant sib it will consume; and so on down the ladder, to the most subordinate chick, which will consume whatever is left over for it. The value $P_{B,\mu}$ will denote the fraction of PI allocated to the μ -th chick in a B -chick brood. The values of the $P_{B,\mu}$ for brood sizes up to 12 are given in table 1 (no larger brood sizes are favored by parents with the parameter values used in the numerical analysis). They are calculated by a straightforward generalization of the process detailed by Forbes (1993, in the appendix). The expected behavior of parents and their offspring differs from one scenario to the other. Hence, whenever such a distinction is necessary, equation numbers will be followed by a D when they refer to despotic allocation and by an E when they refer to equal allocation.

The parents choose their optimal brood size B^* and level of investment $M^*(B^*)$ according to the algorithm described in the appendix, which also provides a calculation of the parents' fitness at their optimum (eq. [A2]). Chicks now consider whether they would benefit from brood reduction (only those chicks that would survive after brood reduction are considered since, as O'Connor [1978] pointed out, chicks will never favor their own death before their parents do). They first calculate their expected inclusive fitness for the parentally favored brood size, B^* (in the case of despotic allocation, because of the existence of a feeding hierarchy, different chicks have different expected inclusive fitness),

$$W_{\text{OFF},\mu}(B^*) = \left(1 - \frac{m_v}{M^*(B^*)P_{B^*,\mu}}\right) + \frac{1}{2} \sum_{v \neq \mu} \left(1 - \frac{m_v}{M^*(B^*)P_{B^*,v}}\right) + \frac{1}{2} \left[1 - \left(\frac{M^*(B^*)}{M_H}\right)^\theta\right], \quad (3, D)$$

$$W_{\text{OFF}}(B^*) = \frac{B^* + 1}{2} \left(1 - \frac{m_v}{M^*(B^*)/B^*}\right) + \frac{1}{2} \left[1 - \left(\frac{M^*(B^*)}{M_H}\right)^\theta\right]; \quad (3, E)$$

and for a brood size smaller by one,

$$W_{\text{OFF},\mu}(B^* - 1) = \left(1 - \frac{m_v}{M^*(B^* - 1)P_{B^* - 1,\mu}}\right) + \frac{1}{2} \sum_{v \neq \mu} \left(1 - \frac{m_v}{M^*(B^* - 1)P_{B^* - 1,v}}\right) + \frac{1}{2} \left[1 - \left(\frac{M^*(B^* - 1)}{M_H}\right)^\theta\right], \quad (4, D)$$

$$W_{\text{OFF}}(B^* - 1) = \frac{B^*}{2} \left(1 - \frac{m_v}{M^*(B^* - 1)/(B^* - 1)}\right) + \frac{1}{2} \left[1 - \left(\frac{M^*(B^* - 1)}{M_H}\right)^\theta\right], \quad (4, E)$$

where $M^*(B^*)$ and $M^*(B^* - 1)$ are given by equations (A1, D) and (A1, E). In the right-hand side of equations (3, D) and (4, D), the first term gives the individual fitness of the chick that is considering the possibility of committing siblicide, the second term is the fitness (weighted by the coefficient of relatedness, assumed to be 0.5) of the other chicks in the brood (before or after siblicide for eqq. [3] and [4], respectively), and the final term is the expected future reproductive success of the parent (once again weighted by the coefficient of relatedness). Chicks will favor brood reduction whenever their fitness in a brood of $B^* - 1$ chicks is greater than in a brood of B^* chicks. For equal allocation of resources, it can be shown (Parker and Mock 1987) that all surviving offspring agree over what the optimal brood size would be. In the case of despotic allocation this is not so, and the expected change in inclusive fitness must be calculated for every chick except the most subordinate one. Assuming that older chicks cannot interfere between their younger siblings (the α chick can force brood reduction, but it cannot prevent the β chick from killing the γ chick), which is consistent with the assumption that parents themselves cannot prevent brood reduction, siblicide occurs whenever any chick in the brood can increase its inclusive fitness by eliminating its youngest sib. This opens the door to a new source of family conflict: when some chicks favor siblicide, others may take sides with their parents in the evolutionary game against the brood reductionists. Nevertheless, assuming that older sibs are

not better than their parents at preventing siblicide, in despotic allocation there will be brood reduction whenever there is $\mu < B^*$ such that

$$\Delta W_{\text{OFF},\mu} = W_{\text{OFF},\mu}(B^* - 1) - W_{\text{OFF},\mu}(B^*) > 0. \quad (5, D)$$

For equal allocation, assuming that there is a clear runt, which if it survives will share resources equally with its sibs and will have an equal probability of joining the breeding population, siblicide will be favored by all the chicks (except the runt) whenever

$$\Delta W_{\text{OFF}} = W_{\text{OFF}}(B^* - 1) - W_{\text{OFF}}(B^*) > 0. \quad (5, E)$$

Numerical Results

By the definition of optimal brood size, parents always decrease their expected inclusive fitness after brood reduction. Hence, there are so far two possibilities: either chicks also experience a decrease in expected inclusive fitness after brood reduction (cooperation is the ESS; Forbes 1993), in which case parents and their offspring agree over optimal brood size, or some of the chicks can increase their inclusive fitness by committing siblicide (there is POC over brood size). We can now compute, for particular values of the model's parameters, the expected inclusive fitness for parents and chicks at brood sizes B^* and $B^* - 1$. I used for this purpose the following parameter values: $M_H = 10, 15, 20,$ and 25 ; $m_v = 1, 2, 3,$ and 4 ; $\theta = 1, 2, 3, 4,$ and 6 ; $f_H = 1, 2, 4, 6,$ and 8 . These include all the values used by Forbes (1993) in his analysis, except for a θ equal to 0.5 : as explained in the original article, values of θ less than one are biologically irrelevant (see below). To explore a greater range of possibilities I have introduced other new values (e.g., data from kestrels, *Falco tinnunculus*, are consistent with a value of θ close to four [table 3 and fig. 9 in Daan et al. 1990]; hence, it seemed logical to use a range of θ values bracketing a θ of four). A plot of the percentage change in expected inclusive fitness for parents,

$$\% \Delta W_{\text{PAR}} = 100 \frac{W_{\text{PAR}}(B^* - 1) - W_{\text{PAR}}(B^*)}{W_{\text{PAR}}(B^*)}, \quad (6)$$

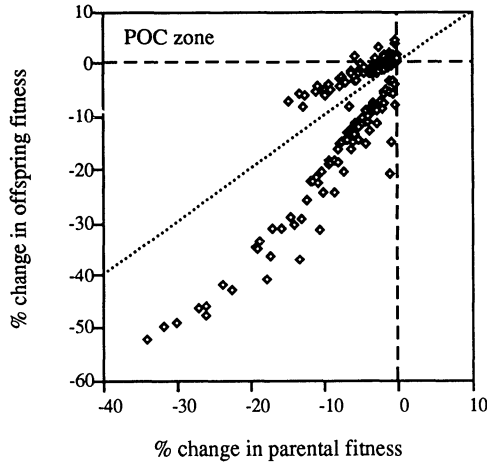
versus the percentage change in inclusive fitness of their offspring (fig. 1),

$$\% \Delta W_{\text{OFF}} = \max_{\mu} \left(100 \frac{W_{\text{OFF},\mu}(B^* - 1) - W_{\text{OFF},\mu}(B^*)}{W_{\text{OFF},\mu}(B^*)} \right), \quad (7, D)$$

$$\% \Delta W_{\text{OFF}} = 100 \frac{W_{\text{OFF}}(B^* - 1) - W_{\text{OFF}}(B^*)}{W_{\text{OFF}}(B^*)}, \quad (7, E)$$

shows the same trend pointed out by Forbes (1993, his fig. 9): cooperation is the ESS more often than conflict, and when there is conflict over brood size, the changes in expected inclusive fitness resulting from siblicide are small. However, the results differ from Forbes's in two ways. First, the overall proportions of cases where there is conflict over brood size (24% for equal allocation and 17.5% for despotic allocation) are greater than the proportions Forbes found (8% for

A)



B)

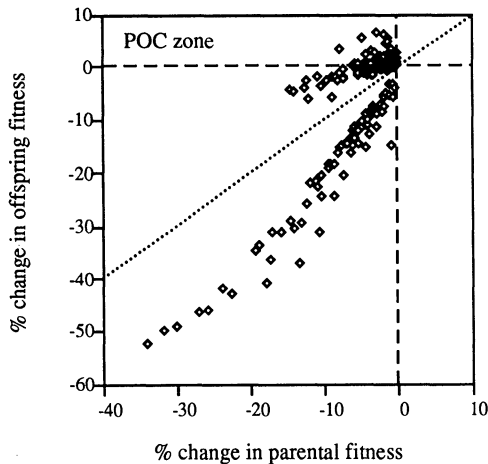


FIG. 1.—Percentage change in inclusive fitness for parents ($\% \Delta W_{\text{PAR}}$) and chicks ($\% \Delta W_{\text{OFF}}$) after brood reduction under despotism (A) and equal (B) distribution of food. All data are shown. Data points in the second quadrant correspond to parent-offspring conflict over brood size (POC zone). The dotted line indicates $\% \Delta W_{\text{PAR}} = \% \Delta W_{\text{OFF}}$.

equal allocation and 5% for despotic allocation). Besides, the fitness increases that chicks can obtain from siblicide (up to 4.3% and 6.3% for equal and despotic allocation, respectively) are greater than those reported by Forbes (up to 2.5%). These differences are due not only to the use of different parameter values (with exactly the same parameter values, there is 14% POC over brood size with equal allocation and 12% with despotic allocation of resources). They arise for three reasons. First, when θ equals 0.5 (the biologically irrelevant value), parents al-

ways do better by forgoing reproduction ($B^* = 0$ in 100% of cases, for equal and despotic allocation of resources). As there can be no POC over brood size in this case, the use of a θ of 0.5 makes it look as if POC was comparatively rare by a dilution effect. Second, Forbes calculates optimal PI level and consequent fitness for broods of size zero to three, then takes as “optimal brood size” the one ensuing in greatest fitness. The optimal brood size for parents, however, is often greater than three ($B^* > 3$ in 24% of equal allocation and 22% of despotic allocation cases studied). In these cases offspring will often benefit from reducing brood size from B^* to $B^* - 1$, but they will seldom benefit from reducing brood size all the way down to two chicks. Third, two of the algebraic errors in Forbes’s theoretical development tend to make POC over brood size look rarer than it is. Forbes’s calculation of PI for $B^* = 3$ and despotic allocation (his eq. [12]),

$$M^*(3) = \left[\frac{m_v(M_H)^\theta}{\theta f_H P_{3\alpha} P_{3\beta} P_{3\gamma}} \right]^{1/(\theta+1)},$$

should read

$$M^*(3) = \left[\frac{m_v(M_H)^\theta}{\theta f_H} \left(\frac{1}{P_{3\alpha}} + \frac{1}{P_{3\beta}} + \frac{1}{P_{3\gamma}} \right) \right]^{1/(\theta+1)}.$$

Because

$$\frac{1}{P_{3\alpha} P_{3\beta} P_{3\gamma}} > \frac{1}{P_{3\alpha}} + \frac{1}{P_{3\beta}} + \frac{1}{P_{3\gamma}},$$

Forbes’s equation (12) overestimates PI and gives a value closer to the offspring maximum than the true parental optimum, hence reducing the scope for POC in despotic allocation. Last, for equal allocation, the threshold for POC should not be

$$\frac{M^*(B)}{m_v} < 2B - 1,$$

as in Forbes’s equation (24), but the less constraining value

$$\frac{M^*(B)}{m_v} < 2B,$$

which explains why Forbes also finds smaller levels of conflict for equal allocation of resources.

Before going any further, let us examine how rare conflict is expected to be according to this model. The data points in figure 1 are clearly divided in two clouds: for one of them $\% \Delta W_{\text{PAR}} < \% \Delta W_{\text{OFF}}$ and for the other $\% \Delta W_{\text{PAR}} > \% \Delta W_{\text{OFF}}$. As shown in table 2, there is a large number of cases for which the optimal brood size is either $B^* = 0$ or $B^* = 1$. These cases are not particularly interesting: when parents do not reproduce or when they have a single offspring, there can be no siblicide. The large number of cases in which the model predicts that parents should forgo reproduction should be considered, if anything, as a

TABLE 2
 CONFLICT AND COOPERATION AFTER THE FIRST MOVE

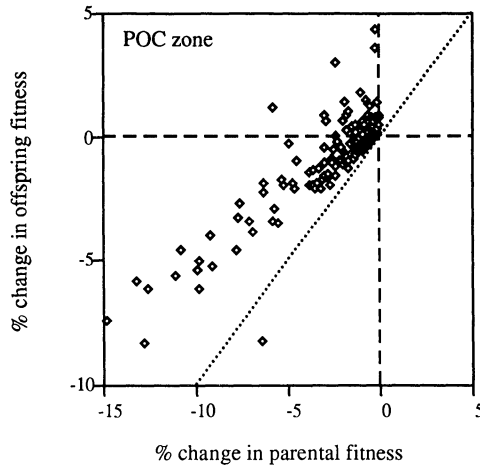
B^*	EQUATION ALLOCATION			DESPOTIC ALLOCATION		
	Number	Conflict	Cooperation	Number	Conflict	Cooperation
≤ 1	198	0	198	209	0	209
2	70	41	29	69	27	42
3	35	18	17	35	13	22
4-5	41	20	21	39	15	24
≥ 6	56	17	39	48	15	33
Total	400	96	304	400	70	330

pathology of the parameter values used. It certainly provides us with little information about siblicide and brood reduction. When broods consist of a single chick, there can be brood reduction but not siblicide. Further, the results from O'Connor's (1978) and Godfray and Harper's (1990) models are still qualitatively true even when adjustment of parental investment is taken care of: the level of resource availability below which brood reduction is favored is highest for surviving offspring, intermediate for the parents, and lowest for the victim. It follows that offspring will never favor brood reduction when $B^* = 1$. Hence, we can leave aside these cases and concentrate on the more interesting situations where $B^* \geq 2$. The picture (fig. 2) now changes dramatically: the $\% \Delta W_{\text{PAR}} > \% \Delta W_{\text{OFF}}$ clouds have, for the most part, disappeared, and conflict is almost as common as cooperation, particularly in the case of equal allocation.

LAST MOVE: EVOLUTIONARY BLACKMAIL

For Forbes (1993) the brood reduction game ends here. It should not be so. So far, the game consists of a starting condition set up by the parents $\{B^*, M^*(B^*)\}$ (the notation $\{B, M\}$ will indicate a strategy set consisting of broods of size B on which parents invest a total of M units of PI) and possibly one more move by each of the players. When cooperation is the ESS, the game is truly over: after the starting conditions are set up, neither chicks nor parents can increase their fitness by a unidirectional move. In case of conflict we have seen that (as long as parents cannot prevent brood reduction from taking place) siblicide will invade and the population will settle at $\{B^* - 1, M^*(B^* - 1)\}$. Is this an ESS? For this strategy set to be an ESS, two conditions must be met (Maynard Smith 1982). One of them was pointed out by Forbes (1993): it is possible that chicks could benefit from a second siblicidal round, leading to a $\{B^* - 2, M^*(B^* - 2)\}$ population. This possibility is logically similar to the first siblicidal round, and it can easily be studied in accordance with the same framework. I will not follow it further. Instead, I will concentrate on the second condition that the strategy set must satisfy to be an ESS: no modification of parental behavior should lead to an increase in their fitness. Clearly, in an ontogenetical time span there is little

A)



B)

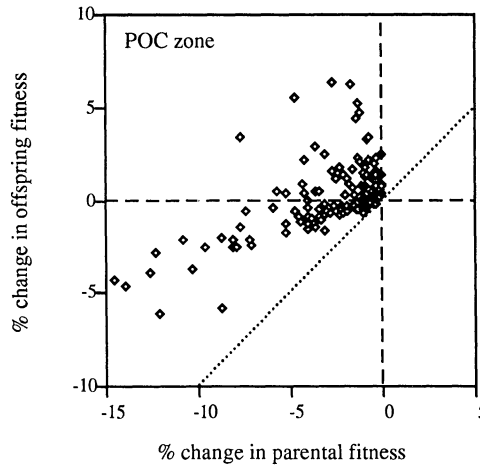


FIG. 2.—Percentage change in inclusive fitness for parents ($\% \Delta W_{\text{PAR}}$) and chicks ($\% \Delta W_{\text{OFF}}$) after brood reduction under despotism (A) and equal (B) distribution of food, with data corresponding to brood sizes equal or less than one removed. Data points in the second quadrant correspond to parent-offspring conflict over brood size (POC zone). The dotted line indicates $\% \Delta W_{\text{PAR}} = \% \Delta W_{\text{OFF}}$.

parents can do, other than readjust investment from $M^*(B^*)$ to $M^*(B^* - 1)$, after their smallest chick is eliminated by its sibs. Natural selection, however, does not work at this time scale. Consider the fate, in a $\{B^* - 1, M^*(B^* - 1)\}$ population, of a mutant that has a starting point $\{B^*, M'\}$ and that after brood reduction (if there is such) settles down to $\{B^* - 1, M^*(B^* - 1)\}$. Will this mutant spread? Because offspring fitness, for any B greater than zero, has a single maximum at

$M_{\text{OFF}} > M^*(B)$, if the mutant parent is providing a level of resources smaller than its own optimum ($M' < M^*(B^*)$), it follows that its offspring will suffer a reduction in fitness with respect to the offspring of wild-type parents ($W_{\text{OFF}}(B^*, M^*(B^*)) > W_{\text{OFF}}(B^*, M')$), and hence

$$\begin{aligned} \Delta W'_{\text{OFF}} &= W_{\text{OFF}}(B^* - 1, M^*(B^* - 1)) - W_{\text{OFF}}(B^*, M') \\ &> W_{\text{OFF}}(B^* - 1, M^*(B^* - 1)) - W_{\text{OFF}}(B^*, M(B^*)) = \Delta W_{\text{OFF}} > 0. \end{aligned} \quad (8)$$

Chicks will still favor brood reduction, the endpoint will be $\{B^* - 1, M^*(B^* - 1)\}$, and the fitness of the mutant individual will be exactly the same as that of wild-type individuals. Hence, the mutation cannot invade by natural selection. This mutation could invade by random drift in small populations, since there is no selection against it, but this possibility will not concern us here.

We must now consider the case of a compliant mutation that yields to the evolutionary blackmail posed by siblicidal chicks by increasing investment in each brood to a point beyond its optimum ($M' > M^*(B^*)$) in an attempt to prevent siblicide. For M' large enough, it is possible that $\Delta W'_{\text{OFF}} \leq 0$. Under these conditions chicks no longer favor brood reduction, and the game ends at $\{B^*, M'\}$. The mutation will invade if the adults' fitness is greater at $\{B^*, M'\}$ than at $\{B^* - 1, M^*(B^* - 1)\}$, that is, if the cost of increasing PI from $M^*(B^*)$ to M' is smaller than the benefit derived from avoiding siblicide. We must therefore calculate, whenever there is a conflict over brood size, the value of M' at which offspring no longer favor brood reduction ($\Delta W'_{\text{OFF}} = 0$). This is done by numerically solving the condition

$$\begin{aligned} &\left(1 - \frac{m_v}{M^*(B^* - 1)P_{B^* - 1, \mu}}\right) + \frac{1}{2} \sum_{v \neq \mu} \left(1 - \frac{m_v}{M^*(B^* - 1)P_{B^* - 1, v}}\right) \\ &+ \frac{1}{2} \left[1 - \left(\frac{M^*(B^* - 1)}{M_H}\right)^{\theta}\right] = \left(1 - \frac{m_v}{M'P_{B^*, \mu}}\right) \end{aligned} \quad (9, D)$$

$$\begin{aligned} &+ \frac{1}{2} \sum_{v \neq \mu} \left(1 - \frac{m_v}{M'P_{B^*, v}}\right) + \frac{1}{2} \left[1 - \left(\frac{M'}{M_H}\right)^{\theta}\right], \\ &\frac{B^*}{2} \left(1 - \frac{m_v}{M^*(B^* - 1)/(B^* - 1)}\right) + \frac{1}{2} \left[1 - \left(\frac{M^*(B^* - 1)}{M_H}\right)^{\theta}\right] \\ &= \frac{B^* + 1}{2} \left(1 - \frac{m_v}{M'/B^*}\right) + \frac{1}{2} \left[1 - \left(\frac{M'}{M_H}\right)^{\theta}\right] \end{aligned} \quad (9, E)$$

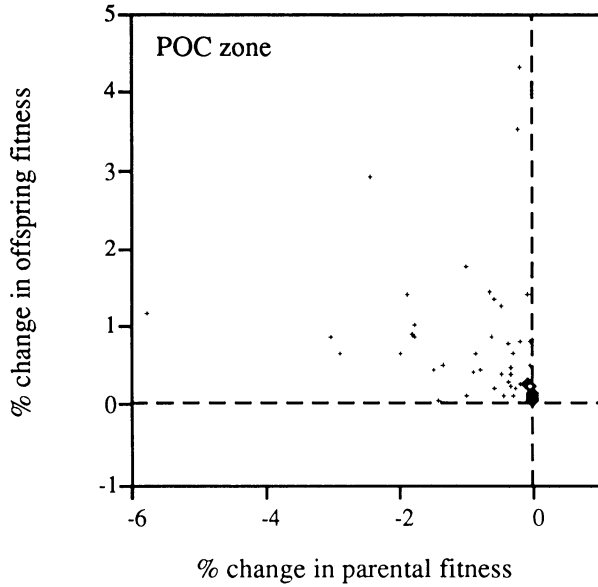
derived from equations (3) and (4). In equation (9, D), μ refers to the chick that benefits most from siblicide. Knowing M' , one proceeds to calculate the change in inclusive fitness experienced by parents as a result of the compliant mutation:

$$\begin{aligned} \Delta W_{\text{PAR}}(\text{compliance}) = & \left(\sum_{\mu=1}^B \left(1 - \frac{m_v}{M' P_{B,\mu}} \right) + f_H \left[1 - \left(\frac{M'}{M_H} \right)^\theta \right] \right) \\ & - \left(\sum_{\mu=1}^{B-1} \left(1 - \frac{m_v}{M^*(B-1) P_{B-1,\mu}} \right) \right. \\ & \left. + f_H \left[1 - \left(\frac{M^*(B-1)}{M_H} \right)^\theta \right] \right), \end{aligned} \quad (10, D)$$

$$\begin{aligned} \Delta W_{\text{PAR}}(\text{compliance}) = & \left(B \left(1 - \frac{m_v}{M'/B} \right) + f_H \left[1 - \left(\frac{M'}{M_H} \right)^\theta \right] \right) \\ & - \left((B-1) \left(1 - \frac{m_v}{M^*(B-1)/(B-1)} \right) \right) \\ & + f_H \left[1 - \left(\frac{M^*(B-1)}{M_H} \right)^\theta \right]. \end{aligned} \quad (10, E)$$

The mutation will invade whenever parental inclusive fitness is increased as a result of compliance ($\Delta W_{\text{PAR}}(\text{compliance}) > 0$). In these cases, is $\{B^*, M'\}$ an ESS? Indeed it is. Because chicks do not benefit from brood reduction any longer, $\{B^*, M'\}$ will be the endpoint of the game. In a $\{B^*, M'\}$ population, parents using a strategy $\{B^*, M''\}$ with M'' less than M' will end up at $\{B^* - 1, M^*(B^* - 1)\}$, where, if $\Delta W_{\text{PAR}}(\text{compliance}) > 0$, their fitness is reduced with respect to the rest of the population. If, on the other hand, M'' is greater than M' , chicks will (normally) not favor siblicide, and $\{B^*, M''\}$ will be the endpoint of the game. Now, since both M' and M'' are greater than $M^*(B^*)$ and parental fitness is decreasing in M for all M greater than $M^*(B^*)$, parents at $\{B^*, M''\}$ will have lower fitness than at $\{B^*, M'\}$: the M'' mutation is not favored in this case either. Finally, if M'' is so large that chicks favor brood reduction, the game ends at $\{B^* - 1, M^*(B^* - 1)\}$ and, as in the case in which M'' is less than M' , the mutation is selected against in a $\{B^*, M'\}$ population. Therefore, whenever there is POC over brood size ($\Delta W_{\text{OFF}} > 0$, eqq. [5]) and $\Delta W_{\text{PAR}}(\text{compliance}) > 0$ (eqq. [10]), compliance is the ESS. Figure 3 shows the percentage fitness change for parents and offspring at the ESS in cases in which there is POC over brood size after the first move of the game. For parents, the change is calculated relative to fitness at $\{B^*, M^*(B^*)\}$ and for chicks relative to fitness at $\{B^* - 1, M^*(B^* - 1)\}$. It clearly shows two things: compliance is very seldom the ESS, and, when it is, fitness changes derived from it are very small. The smallness of these changes, however, should not be misinterpreted: from the point of view of the parents, the smaller the deviation from maximum fitness, the greater the payoff of compliance. As figure 4 shows, by increasing their PI level, parents can sometimes avoid a rather costly brood reduction by paying a very small price.

A)



B)

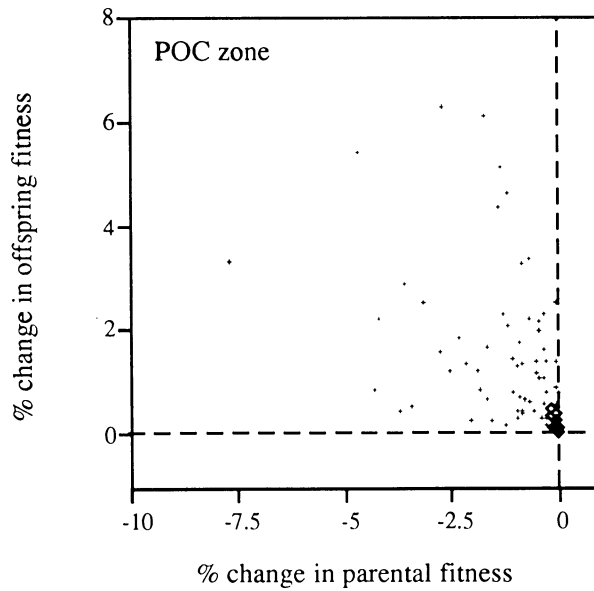
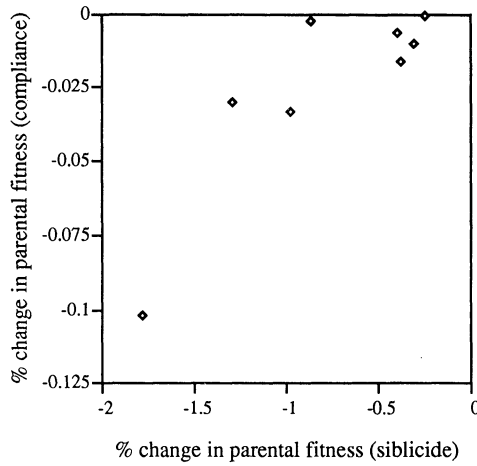


FIG. 3.—Percentage change in inclusive fitness for parents ($\% \Delta W_{\text{PAR}}$) and chicks ($\% \Delta W_{\text{OFF}}$) at the ESS for despotic (A) and equal (B) distribution of food in cases of POC over brood size. The ESS can be siblicide (*diamonds*) or compliance (*crosses*). When compliance is the ESS, parents manage to maintain their desired brood size at an exceedingly small cost.

A)



B)

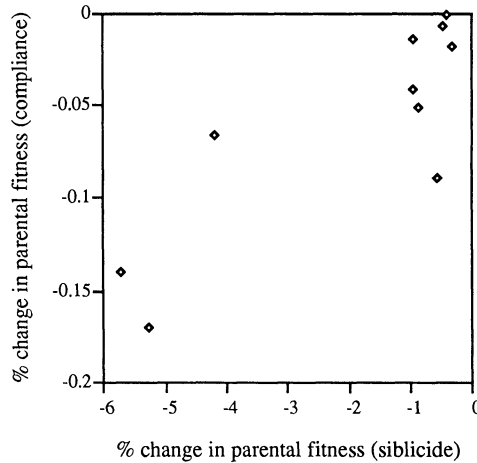


FIG. 4.—Percentage change in parental inclusive fitness owing to increased parental investment ($\% \Delta W_{\text{PAR}}(\text{compliance})$) versus percentage change in inclusive fitness for parents owing to siblicide ($\% \Delta W_{\text{OFF}}(\text{siblicide})$) when compliance is the ESS for the despotic (A) and the equal (B) distribution of food. Notice the difference in scale between the axes.

DISCUSSION

Quibble or Conflict?

We have already noticed that, when only relevant brood sizes are considered, POC over brood size is a very common prediction of the model. As Forbes (1993) noticed, the differences in inclusive fitness, both for parents and their offspring, are normally of a few percent of maximum attainable fitness. Forbes concludes

from this that “offspring are exploiting parental indifference over brood size when they succeed in increasing their fitness through brood reduction” (p. 105). But are they really? Considering only those broods where there is POC, the percentage decrease in parental fitness due to brood reduction (with the parameter values considered in the analysis) is 1.04 ± 1.25 (mean \pm SD) under despotic and 1.54 ± 1.72 under equal allocation, while the respective percentage increases in offspring fitness are 0.97 ± 1.12 and 1.74 ± 1.81 . If one party is indifferent about brood size, it is unclear whether it should be the parents or their offspring.

Second, how big must a cost or benefit associated with some trait be in order to impose a selection pressure on that trait? This is neither a new nor an easy question. The answer depends on a number of factors, one of the key ones being the population structure. Forbes seems to imply that a cost of the order of 2% will not be enough to select for new parental behaviors preventing siblicide. As Haldane (1932) pointed out, however, in large populations any advantageous mutation, no matter how small an advantage it confers, has a finite probability of survival and invasion. Thus, the smallness of the fitness increments is not, in itself, enough reason to conclude that adaptations to prevent siblicide are not to be expected: if a mutation allowing parents to prevent siblicide appeared often enough, it would spread. Another question is whether other factors not considered in the model would have such a large impact as to make brood size an essentially irrelevant issue. This is, in principle, possible. However, a large body of evidence supports the view that there is a strong selective pressure on getting brood size “right” (Tinbergen and Daan 1990; see Dijkstra et al. 1990 for a review), and one of the main factors that have not been considered in either this or the original model is environmental variability. Fluctuations in the environment make chicks more prone to commit siblicide (Forbes and Ydenberg 1992), and this will tend to make POC more, rather than less, common (Forbes 1993).

Another issue that the model leaves aside are the cost of laying and incubating the extra egg from which the victim chick will hatch and the cost of feeding a supernumerary chick for what may be considerable lengths of time. Certainly, when siblicide is about to take place, the parents must not take into consideration how much they have spent on it but, rather, should evaluate the costs and benefits of keeping it alive. At the evolutionary level, however, things are otherwise, and we must keep in mind that one of the main paradoxes in siblicidal behavior is why parents so readily pay the cost of laying and incubating an extra egg that has such a small probability of becoming an adult bird. The answer to this question must lie in the stochasticity of the environment, and this deterministic model does little to answer it. Indeed, in a deterministic environment, any cost associated with laying (and there is growing evidence that laying may be more costly than was once assumed; Heaney and Monaghan 1995; Monaghan et al. 1995) will result in clutch sizes smaller than expected in the absence of sibling competition: instead of laying B^* eggs, allowing siblicide to occur, and adjusting their level of investment to the ensuing brood of $B^* - 1$ chicks, parents would lay $B^* - 1$ eggs from the beginning. This decrease in optimal clutch size due to sibling competition is equivalent to the one obtained by Godfray and Parker (1992) in a different context. It should be clear from this discussion that, although determin-

istic models help us understand some aspects of the evolution of siblicide, the definite answer must lie in stochastic models (Forbes 1993; Godfray 1995a).

Evolutionary Blackmail

An important concept added in this article to the brood reduction game is that of the evolutionary blackmail. When parents and offspring favor different brood sizes, the conflict could be resolved in a number of ways. At one extreme, older chicks would eliminate their siblings one way or another without readjustment of parental investment (offspring win). At the opposite extreme, parents would prevent siblicide without altering per-brood investment (parents win). The case in which offspring win is not an ESS because parents would immediately be selected to reduce investment in current brood. This model assumes throughout that the case in which parents win is unattainable: parents cannot interfere in their offspring's endeavors (this assumption may not be completely justified and will be discussed below). In between these two extremes lie two possible ESSs: brood reduction with reduced parental investment and compliance to the evolutionary blackmail. Both ESSs are compromises in the sense that parent and offspring fitnesses at the ESS are smaller than at their favored extremes. For a particular set of parameter values, only one of these two strategies will be an ESS. Which one is the ESS is determined from the difference in parental fitness between them, since the fitness of surviving offspring is equal for both strategies and the victim of brood reduction is assumed unfit to prevent its own death.

Under which conditions can the blackmail work? It is probably important to start by stressing when it will not work. For example, imagine a situation in which both parents and offspring agree over brood size. Parents will lay their preferred clutch size, B^* , and will invest in their brood the amount of resources $M^*(B^*)$ that maximizes their fitness. Offspring, however, would be better off if parental investment increased to some level $M' > M^*(B^*)$. They could propose the following gambit to their parents: "Either you increase per-brood investment from $M^*(B^*)$ to M' or we eliminate the weaker chick of the brood." This type of mutation would not spread. Mutants in the population would encounter wild-type parents providing $M^*(B^*)$ to the brood. The mutants would then commit siblicide, parents would decrease investment in their brood, and the fitness of the mutant chicks would be smaller than that of wild-type chicks. The blackmailing mutants would soon be eliminated from the population. Therefore, a necessary condition for the blackmail-compliance strategies to invade a population is that offspring must favor brood reduction in the absence of compliant parents. In another example, compliance would not work in obligate brood reductionist populations either. Consider a population in which parents always lay two eggs, only to see their older or stronger chick eliminate the other. Could they avoid brood reduction by providing more food to the brood? Not if siblicide is hardwired and unconditional. If older chicks kill their younger siblings no matter how much food they get (Kepler 1969; Gargett 1978), a compliant parent mutant will not be selected for because its compliance will be without effect. Hence, for compliance to invade a brood reductionist population, the behavior of the chicks must be influenced by the amount of food they receive. This is probably the case in facultative brood

reductionist species: in blue-footed boobies (*Sula nebouxii*), experimentally induced hunger results in an increased level of sibling aggression (Drummond and García Chavelas 1989). If brood reduction takes place when parental investment falls below some threshold, parents can prevent brood reduction by increasing brood provisioning. Compliance will therefore be able to invade the population if the costs to the parents of the extra provisioning (reflected in the model by the values of θ and M_H) do not exceed the benefits of maintaining their preferred brood size. Notice that for compliance to invade a siblicidal population, aggression levels themselves need not decrease as food provisioning increases. Thus, in great egrets (*Casmerodius albus*), the intensity of aggressive behavior is not inversely related to brood provisioning levels, but siblicide is (presumably because better-fed junior chicks are more likely to defend themselves from their older sibs' attacks; Mock et al. 1987), which allows for a compliant strategy to be effective.

The same principle described here for blackmailing and compliance between parents and their offspring applies equally to sib-sib conflicts over brood size under despotic allocation of resources. I will describe the principle for three-chick broods to avoid unnecessary abstraction, but it can be applied to any brood size greater than two. In a three-chick brood, the α chick will normally consume 41% of the food provisioned, the β chick 35%, and the γ chick the remaining 24% (table 1). Imagine now that both the parents and the α chick maximize their fitness with a brood of size $B = 3$, while the β chick favors $B = 2$. As we have seen, parents will sometimes be selected to work harder to save their preferred brood size. Alternatively, the α chick could be selected to reduce its own share of food to a point where the β chick no longer favors brood reduction.

With the particular fitness functions used by this model (eqq. [1] and [2]), the compliant strategy is of little practical importance. In most cases, equations (9) have no solution at all: no matter how much parents invest in a brood of B^* chicks, offspring fitness will be greater in a brood of $B^* - 1$ chicks that receives the parentally optimal level of resources (fig. 5). Equations (1) and (2), however, were not initially chosen for their biological content but, rather, for mathematical tractability. I have used them throughout to make comparisons with Forbes's (1993) results possible. Other fitness functions will readily lead to different results. This is not merely wishful thinking: substituting

$$f(M) = \begin{cases} f_H & \text{if } M \leq 0 \\ f_H \sqrt{1 - \left(\frac{M}{M_H}\right)^\theta} & \text{if } 0 < M < M_H \\ 0 & \text{if } M_H \leq M \end{cases} \quad (11)$$

and

$$\rho(m) = \begin{cases} 1 - e^{-\omega(M/B - m_v)} & \text{if } m > m_v \\ 0 & \text{if } m \leq m_v \end{cases} \quad (12)$$

for equations (1) and (2) (where all variables are defined as before and ω is the rate at which the probability of joining the breeding population approaches its

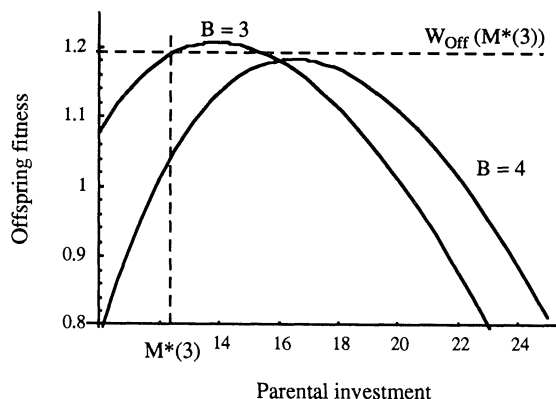


FIG. 5.—Relationship of parental investment and offspring fitness. When offspring fitness is greater for a $(B^* - 1)$ -chick brood and $M^*(B^* - 1)$ units of PI ($W_{\text{OFF}}(M^*(3))$, dashed horizontal line) than for a B^* -chick brood and any level of PI, compliance will not work: parents will not be able to prevent brood reduction by increasing provisioning levels ($B^* = 4$ in this example). The dashed vertical line represents PI for a three-chick brood, $M^*(3)$.

asymptotic value) and using the parameter values $M_H = 10, 15, \text{ and } 20$; $m_v = 1, 2, \text{ and } 3$; $\theta = 2, 3, \text{ and } 4$; $f_H = 2, 4, 6, \text{ and } 8$; and $\omega = 1, 2, \text{ and } 3$, under the assumption of equal allocation of resources, one finds that there is POC over brood size in 21.6% (61 of 283) of the cases in which B^* is greater than one, and compliance is the ESS in 26.2% (16 of 61) of the cases in which there is POC over brood size. Given that by and large we do not know the precise shape of fitness functions, we should certainly entertain the possibility that compliance is a biologically meaningful strategy.

As for the sib-sib conflicts mentioned above, according to which α chicks might agree with their parents over brood size while β chicks favor brood reduction, they do not become apparent with the parameter values studied and the fitness functions given by equations (1) and (2). Once again, this is not a general property, and there is no guarantee that other fitness functions will lead to the same conclusions. In fact, even with the particular functions used here, sib-sib conflicts would appear if the parameter values favored greater brood sizes. It can be shown that the probability that the μ -th chick disagrees over brood size with its parents under despotic allocation of resources (with our choice of fitness functions) increases with the ratio between the proportion of food that the μ -th chick receives in a $(B - 1)$ - and in a B -chick brood, $r(B, \mu) = P_{B-1, \mu} / P_{B, \mu}$. These ratios can be computed from the values given in table 1: because for all B less than 10 this ratio is greatest for the α chick, so long as B is less than 10 there will be no sib-sib conflict over brood size, since either the α chick favors brood reduction or no one does. Hence, only with brood sizes greater than 10 could we possibly see sib-sib conflicts. These brood sizes are not common in bird species but might be important if we want to apply these concepts to other taxa.

Siblicide and Brood Size

As far as the conditions for siblicide are concerned, O'Connor's (1978) and Godfray and Harper's (1990) conclusions are qualitatively supported: brood re-

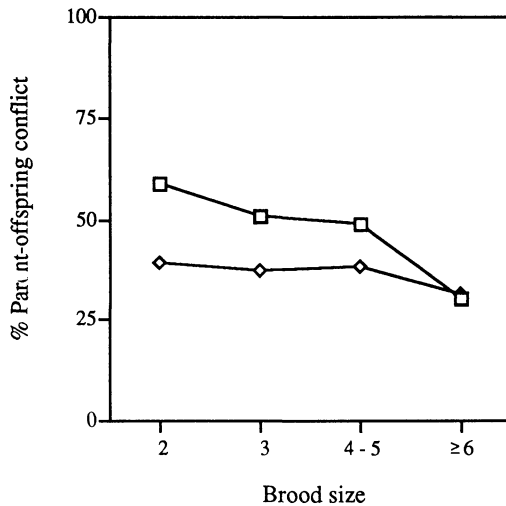


FIG. 6.—Relationship of POC and brood size. The incidence of POC over brood size (shown as a percentage of occurring cases) is a decreasing function of brood size with equal allocation of resources (*squares*) but independent of brood size under despotic allocation (*diamonds*).

duction is most likely to be favored by surviving offspring, followed by parents, and only last by the victims. Quantitatively, however, the span of the conflict is reduced by parental readjustment of investment (Forbes 1993): the number of environments (parameter values in the model) where POC is expected is smaller when parental readjustment of investment is taken into consideration than when fixed parental investment is assumed. Moreover, if readjustment of parental investment after brood reduction is incorporated, the idea that POC should be more pronounced in smaller broods (O'Connor 1978; Godfray and Harper 1990; Forbes 1993) is not strongly supported (fig. 6): although conflict decreases as brood size increases under equal allocation, it is essentially independent of brood size under despotic allocation.

Information Transfer

Finally, I will discuss the subject of optimality and perfect information. The model species can be used to calculate precisely the optimal brood sizes and ESS behavioral strategies. This is so because its inclusive fitness is delivered neatly packed in mathematical constructs (eqq. [1] and [2]) and the environments where it lives are precisely described by a set of parameters. However, real birds and their young may face a somewhat different situation. In particular, young may find it difficult to assess the relationship between provisioning rates and parental investment (Trivers 1974): in the model, both quantities have been described by the same variable, which implies a one-to-one relationship between them; in variable environments, however, the parental investment required to obtain a given amount of food is likely to change from year to year (Forbes 1993). Likewise,

parents may not be able to assess accurately the condition of their young, which is most likely to be an influential factor in determining fitness functions. It has been suggested (Drummond et al. 1986) that this could lead to parents adopting a laissez-faire policy: not knowing precisely which brood size they would benefit most from, they might let their offspring sort things out, on the assumption that offspring may be more able than parents to estimate their own optimal brood size and that, since offspring and parental optima are not too far apart, parents may be better off going along with the offspring-estimated optimum. This is plausible. Alternatively, parents might monitor aggression levels as an indicator of brood needs. This would allow them to estimate their optimal brood size, and, in the event of escalating sibling aggression, they could increase parental investment in the brood (compliance) to prevent brood reduction. When favoring brood reduction, they would simply let their stronger chick accomplish the deed. If parents use aggression levels as an indicator of need, however, aggression would immediately start to play two roles: that of signaling and that of determining food allocation in the brood. One could imagine that this double role would lead to an escalation of aggression levels as chicks tried to manipulate their parents into bringing more food to the nest. This need not be the case: as shown by Grafen (1990), if there is a cost associated with aggressive behavior, a stable signaling system could be established. Indeed, it could work very much like the begging situation modeled by Godfray (1995*b*).

Does this mean that parents are completely blind to the conditions of their offspring? Probably not: parents have firsthand information about how much food they provide to the nest. Even though they probably have no direct access to their young's internal state because of individual variability in metabolic processes, parents can probably estimate reasonably well whether they would benefit from brood reduction or not. There is anecdotal evidence that this might be the case in both bird and mammal species. In an experiment to test the effect of food deprivation on brood dominance in blue-footed boobies (Rodríguez-Gironés et al. 1996), chicks received different feeding treatments (wearing neck collars to prevent food ingestion) before being introduced in vacated foster nests in pairs. In 10 of 20 experimental nests, one of the introduced chicks had been food deprived for 32 h. Food-deprived chicks showed significantly more aggression than control chicks and, in three of the 10 nests containing a food-deprived chick, the brooding female cut short their prolonged pecking by pecking the food-deprived chick on the head while it was attacking its foster sib. In all three cases, the females interfered with chick aggression after an attempt to feed the food-deprived chicks: fish was transferred from the female to the food-deprived chick, which was unable to swallow it because of the neck collar and eventually dropped the fish on the ground. It then proceeded to attack its nest mate until it was itself attacked by its foster mother. Other reports of parental interference in sibling aggression come from similar experiments (Drummond and García Chavelas 1989; Mock and Forbes 1992; Drummond 1993) and from South Polar skuas (*Catharacta maccormicki*, Young 1963; Spellerberg 1971). They suggest that parents will try to prevent siblicide if brood reduction will clearly be against their interests. An even more compelling example comes from a study on spotted hyenas (*Crocuta cro-*

cuta) in the Serengeti (H. Hofer and M. L. East, personal communication). Breeding females have singleton or twin litters, and growth rates are significantly reduced in twin litters with respect to singleton cubs. Siblicide is facultative in male-male or mixed-twin litters, but it appears obligate in female-female litters under normal food supply conditions. Adults never interfere in sibling aggression. One season when food was particularly plentiful, a breeding hyena gave birth to two female cubs and prevented the cubs from attacking each other by keeping them in separate birth dens.

ACKNOWLEDGMENTS

I thank H. Drummond, L. S. Forbes, and H. C. J. Godfray for comments on the manuscript. This work was funded by a doctoral fellowship from the Dirección General de Investigación Científica y Técnica (Spain). The model has benefited from firsthand experience with siblicide in blue-footed boobies, which was made possible by the Association for the Study of Animal Behaviour (travel grant, 1993) and the British Ecological Society (research travel grant, September 1994).

APPENDIX

CALCULATING THE OPTIMAL BROOD SIZE: PARENTS' PERSPECTIVE

1. Let $B = 0$. Calculate parental expected inclusive fitness from skipping reproduction:
 $W_{\text{PAR}}(B = 0) = f_H$.
2. Let $B = B + 1$.
 - a) Calculate the optimal level of PI for the new brood size, $M^*(B)$:

$$M^*(B) = \begin{cases} \left[\frac{m_v(M_H)^\theta}{\theta f_H} \sum_{\mu=1}^B \frac{1}{P_{B,\mu}} \right]^{1/(\theta+1)} & \text{if } M^* P_{B,B} \geq m_v \\ 0 & \text{if } M^* P_{B,B} < m_v, \end{cases} \quad (\text{A1, D})$$

$$M^*(B) = \begin{cases} \left[\frac{m_v(M_H)^\theta B^2}{\theta f_H} \right] & \text{if } M^* \geq m_v B \\ 0 & \text{if } M^* < m_v B. \end{cases} \quad (\text{A1, E})$$

- b) Calculate the expected inclusive fitness for this brood size and a PI level of $M^*(B)$,

$$W_{\text{PAR}} = \sum_{\mu=1}^B \left(1 - \frac{m_v}{M^*(B) P_{B,\mu}} \right) + f_H \left[1 - \left(\frac{M^*(B)}{M_H} \right)^\theta \right], \quad (\text{A2, D})$$

$$W_{\text{PAR}} = B \left(1 - \frac{m_v}{M^*(B)/B} \right) + f_H \left[1 - \left(\frac{M^*(B)}{M_H} \right)^\theta \right]. \quad (\text{A2, E})$$

- c) If the newly calculated inclusive fitness is greater than the former one (i.e., for a brood size smaller by one chick), go back to the beginning of step 2. Otherwise, the optimal brood size (strictly speaking, this is the optimal brood size only from the parents' point of view; for brevity, however, I will simply call it optimal brood

size) and PI level are $B^* = B - 1$ (i.e., the brood size from the previous iteration of step 2) and $M^* = M^*(B^*)$.

LITERATURE CITED

- Daan, S., C. Dijkstra, and J. M. Tinbergen. 1990. Family planning in the kestrel (*Falco tinnunculus*): the ultimate control of covariation of laying date and clutch size. *Behaviour* 114:83–116.
- Dijkstra, C., A. Bult, S. Bijlsma, S. Daan, T. Meijer, and M. Zijlstra. 1990. Brood size manipulations in the kestrel (*Falco tinnunculus*): effects on offspring and parent survival. *Journal of Animal Ecology* 59:269–285.
- Drummond, H. 1987. A review of parent-offspring conflict and brood reduction in the Pelicaniformes. *Colonial Waterbirds* 10:1–15.
- . 1993. Have avian parents lost control of offspring aggression? *Etología* 3:187–198.
- Drummond, H., and C. García Chavelas. 1989. Food shortage influences sibling aggression in the blue-footed booby. *Animal Behaviour* 37:806–819.
- Drummond, H., E. González, and J. L. Osorno. 1986. Parent-offspring cooperation in the blue-footed booby (*Sula nebouxi*): social roles in infanticidal brood reduction. *Behavioral Ecology and Sociobiology* 19:365–372.
- Forbes, L. S. 1993. Avian brood reduction and parent-offspring "conflict." *American Naturalist* 142:82–117.
- Forbes, L. S., and R. C. Ydenberg. 1992. Sibling rivalry in a variable environment. *Theoretical Population Biology* 41:135–160.
- Gargett, V. 1978. Sibling aggression in the black eagle in the Matopos, Rhodesia. *Ostrich* 49:57–63.
- Godfray, H. C. J. 1995a. Evolutionary theory of parent-offspring conflict. *Nature (London)* 376:133–138.
- . 1995b. Signaling of need between parents and young: parent-offspring conflict and sibling rivalry. *American Naturalist* 146:1–24.
- Godfray, H. C. J., and A. B. Harper. 1990. The evolution of brood reduction by siblicide in birds. *Journal of Theoretical Biology* 145:163–175.
- Godfray, H. C. J., and G. A. Parker. 1992. Sibling competition, parent-offspring conflict and clutch size. *Animal Behaviour* 43:473–490.
- Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology* 144:517–546.
- Haldane, J. B. S. 1932. *The causes of evolution*. Longmans, Green, London.
- Heaney, V., and P. Monaghan. 1995. A within clutch trade-off between egg production and rearing in birds. *Proceedings of the Royal Society of London B, Biological Sciences* 26:361–365.
- Kepler, C. 1969. The breeding biology of the blue-faced booby (*Sula dactylatra personata*) on Green Island, Kure. *Publications of the Nuttall Ornithological Club* 8:1–97.
- Lack, D. 1947. The significance of clutch size. *Ibis* 89:302–352.
- Lamey, T. C., and D. W. Mock. 1991. Nonaggressive brood reduction in birds. *Acta XX Congressus Internationalis Ornithologici* 1741–1751.
- Magrath, R. D. 1989. Hatching asynchrony and reproductive success in the blackbird. *Nature (London)* 339:536–538.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. Cambridge University Press, Cambridge.
- Mock, D. W., and L. S. Forbes. 1992. Parent-offspring conflict: a case of arrested development. *Trends in Ecology & Evolution* 7:409–413.
- Mock, D. W., and T. C. Lamey. 1991. The role of brood size in regulating egret sibling aggression. *American Naturalist* 138:1015–1026.
- Mock, D. W., T. C. Lamey, and B. J. Ploger. 1987. Proximate and ultimate roles of food amount in regulating egret aggression. *Ecology* 68:1760–1772.
- Mock, D. W., H. Drummond, and C. H. Stinson. 1990. Avian siblicide. *American Scientist* 78:438–449.
- Monaghan, P., M. Bolton, and D. C. Houston. 1995. Egg production constraints and the evolution

- of avian clutch size. *Proceedings of the Royal Society of London B, Biological Sciences* 259:189–191.
- O'Connor, R. J. 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide? *Animal Behaviour* 26:79–96.
- Parker, G. A., and D. W. Mock. 1987. Parent-offspring conflict over clutch size. *Evolutionary Ecology* 1:161–174.
- Ricklefs, R. E. 1965. Brood reduction in the curve-billed trasher. *Condor* 67:505–510.
- Rodríguez-Gironés, M. A., H. Drummond, and A. Kacelnik. 1996. Effect of food deprivation on dominance status in blue-footed booby (*Sula nebouxii*) broods. *Behavioral Ecology* 7:82–88.
- Spellerberg, I. F. 1971. Breeding behaviour of the McCormick skua *Catharacta maccormicki* in Antarctica. *Ardea* 59:189–230.
- Tinbergen, J. M., and S. Daan. 1990. Family planning in the great tit (*Parus major*): optimal clutch size as integration of parent and offspring fitness. *Behaviour* 114:161–190.
- Trivers, R. L. 1974. Parent-offspring conflict. *American Zoologist* 14:249–264.
- Young, E. C. 1963. The breeding behaviour of the South Polar skua, *Catharacta maccormicki*. *Ibis* 105:203–233.

Associate Editor: H. C. J. Godfray