# USING A GAME THEORETICAL APPROACH FOR EXPERIMENTAL SIMULATION OF BROOD REDUCTION

## *Conflict and co-operation, effect on brood size with limited resources*

Fredrik Åhman, Lars Hillström

*Department of mathematics natural and computer sciences, University of Gävle, 801 76 Gävle, Sweden*

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Abstract: A number of hypothesis have been presented to explain the complex interactions occurring during brood reduction, but few simulation models successfully combines hypothesis together necessary to describe evolutionary stable strategies. In our solution we present a simple experimental simulation for brood reduction for which each sibling act as an autonomous agent that has the ability to initiate actions for co-operation and competition against others chicks within the same brood. Agents have a limited set of actions that can be activated during the onset of some environmental condition. Parameters for food distribution are determined on a basis of a former known theory for maximizing inclusive fitness. During the experimental simulations we have studied size and fitness measures with varying degree of asynchrony and prey density for siblings within the artificial brood. Results from the experimental simulation shows interesting similarities with brood reduction in a real world setting. Agents within the artificial brood respond with competitiveness whenever resources are limited. Simulated later hatching also showed a lower rate of survival because of natural size hierarchy to co-siblings within the simulated brood.

# 1 INTRODUCTION

A number of hypothesis have been presented to explain causes of brood reduction but few simulation models successfully combines important parameters from each hypothesis together necessary to describe evolutionary stable strategies. In intra-familiar conflicts there is always a trade off between degree of selfishness and altruistic behaviours serving the benefits to the next sibling in the brood (Krebs, Davies, 1984). This trade-off is also well known from the Hamilton equation (1) (Bergstrom ref to Hamilton, 2000) where relatedness ( r ) and benefits (b) is compared to cost for co-operation (c).

$$rb - c > 0 \qquad (1)$$

Mock et al, 1998 describes an interesting optimization problem for fitness in which the degree of selfishness is balanced against the interest of maximizing inclusive fitness for the whole brood. Mocks theory describes a simplistic relationship between total parental investment (M) and portions of (M) for siblings ($m_A$), ($m_B$). If portions of prey could do twice as much use for one of the co-siblings within the same brood its in the dominant chicks best interest to pass that portion on to the next sib. Dependent on relatedness between chicks the portion of the meal passed on can vary in size. Mock et al, 1998 shows optimisation for full siblings which means that relatedness is always 0.5.

In a brood with two siblings portions of parental investment (PI) can be split into p*M for the dominant chick A and (1-p)*M for the subordinate chick B. Mock tries to find a value (p) that maximize fitness for the most dominant chick. The fitness curve f(m) (2) describes an exponential relationship between parental investment (m) and fitness f(m). Increase is very in the beginning of the curve but will slow down as the amount of investment approaches maximum amount (M).

$$f(m) = 1 - \exp(1 - k(m - m\min)) \qquad (2)$$

Mock believe that there is a value of portion (p) in which the remains (1-p) comes in better use for the co-sibling B. The equation describes a relationship between the first partial order derivate where increase of fitness for the dominant A-chick should be equivalent to the double increase of fitness for the B-chick (3).



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$$f'(m_A) = 1/2\, f'(m_B) \tag{3}$$

## 1.1 Conflicting versus co-operative behaviours

Combining conflicting behaviours with co-operating behaviours such as portioning foods to co-siblings seems to be an appealing game theoretical approach. In order to maximize fitness individual interests are likely to be balanced to the benefit of the whole brood. Environmental changes such as variation in prey density and climate variation demands good strategies for survival (Temme, Charnov, 1987). When food abundance is low resources must be carefully invested to maximize reproductive output (Ploger, Mock, 1986).

Controlled brood reduction through hatching asynchrony is often initiated by parents when environmental conditions are less beneficial (Vinuela, 2000; Lamey, Mock, 1991). Hatching asynchrony plays a major role in sibling size hierarchy where the first hatched chick often has total control of food resources due to its large size. Sibling competition will be less frequent because of the natural dominance of the elder chick (Lamey, Mock, 1991).

## 1.2 Theoretical framework for the experimental simulation

Our aim with this work is to build an experimental simulation model for brood reduction. The underlying theory for the game theoretical approach is based on Mock & Parkers earlier work on intra-familiar parent-offspring conflict (Mock et al, 1998). Our experimental model is based on a number of assumptions that is originally inspired by the food and egg viability hypothesis that effects hatching asynchrony (Vinuela, 2000).

We view each sibling is as an agent able to make its own decisions for competition and food ingestion. The agent behaviours is controlled by its characteristics such as aggressiveness and strategy selection for competitive games.

# 2 METHODS

We have chosen to evaluate the agents response to three different variables namely access to prey, hatching asynchrony and rankings within the sibling hierarchy. Each agent is activated by starting a new thread for the corresponding chick. In our game simulation sibling hierarchy is dependent on the number of winnings in conflicts. Chicks winning many conflicts will conquer favourable positions during feeding. The dominant chick is always controlling the amount of food distributed similar to (Mock et al, 1998).

After each feeding data is stored about the chicks size, fitness, minimum mass for starvation and ranking. Feeding is repeated iteratively until chick is ready for fledging or may have deceased due to starvation. The simulation procedure is repeated ten times for each parameter setting.

## 2.1 The simulation platform

We have chosen to implement the brood simulation platform in Java. The Java language is object oriented and supports threading which is needed if we want agents within our simulation environment to act independently. A maximum number of three siblings act simultaneously in our nestling environment. Each sibling can initiate two basic behaviours namely consume() and compete(). Winning a competition means higher ranking. Higher ranking means higher probability for food.

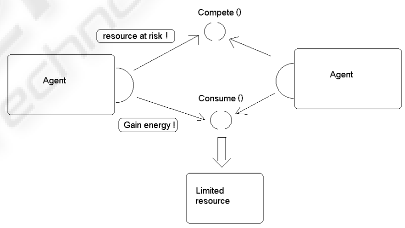



Figure 1: Agent interaction with two basic behaviours {consume, compete}

From a game theoretical perspective we can view the consumption of food as a simple consumer/producer problem where we have a number of consumers that are dependent on a limited resource. In our simulated environment food items is delivered regularly. Upon delivering food the most dominant contestant will take its share first and then left the remains its co-siblings.

## 2.2 Game theory and strategy selection

For each game contestants can choose to alter between different strategies for survival. Common strategies are transgress or retreat. Each chosen strategy has its obvious payoffs and costs dependent on the outcome of the game.

In a game where each opponent can choose between two strategies four combination of payoffs are possible as seen in (Krebs, Davies 1984). If one player choose to retreat ( R ) the cost for that player will be zero or minimum even if he looses the game. The same goes for the opponent who is winning the game. However if both players choose to transgress the cost for each player will affect their immediate fitness with cost –c1, -c2. Gains during winning are described as g1, g2.

A winning in our simple game means higher ranking and therefore better positioning within the nest whenever prey is delivered. A dominant chick in our game determines how food portions to pass on to other subordinate chicks in order to maximize its own inclusive fitness. This works exactly the same as the method used for portioning prey as seen in (Mock et al 1998).

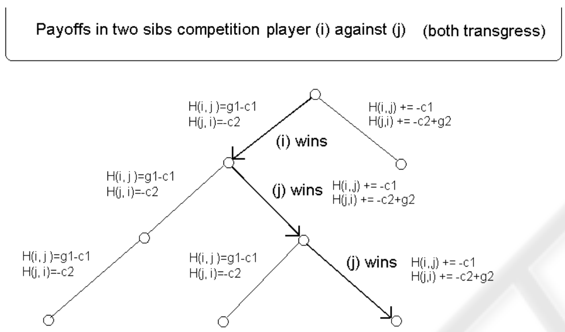



Figure 2: Payoffs in two-player games with fixed strategies

The following equations is taken from (Mock et al 1998).

1. For two sibling games :

A:s portion of prey is (p)
B:s portion of prey is (1-p)

$$f(m_A, m_B) = f(m_A) + \frac{1}{2} f(m_B) \quad (4)$$

$$\frac{\partial[f(m_A) + \frac{1}{2} f(m_B)]}{\partial p} = 0 \quad (5)$$

2. For three sibling games :

A:s portion of prey: $m_A$=Mq
B:s portion of prey : $m_B$=Mp(1-q)
C:s portion of prey : $m_C$=M(1-p)(1-q)

$$f(m_A, m_B, m_C) = f(m_A) + \frac{1}{2} f(m_B) + \frac{1}{2} f(m_C) \quad (6)$$

$$\frac{\partial[f(m_A) + \frac{1}{2} f(m_B) + \frac{1}{2} f(m_C)]}{\partial p} = 0$$

In extension to the two above equations a logistic sigmoid function was added to calculate mass m(w) (7) with respect to intake of energy (w) which is the transfer function for most birds (Ricklefs 1969). Both (L) and k are constants representing bias and increase in growth.

$$m(w) = \frac{1}{1 + Le^{-k*w}} \quad (7)$$

## 3 THE PROBABILISTIC MODEL

As our model is based on former known theories about sibling rivalry and intra-familiar conflicts we need to state predictions about how the agent will respond to certain conditions within the environment. Such events could be lower resource such as lower prey intensity, lower size advantage etc.

### 3.1 Sibling size hierarchy and likelihood to win a conflict

Siblings that have a size advantage is more likely to win a conflict because of less resistance from the minor chick (Smith, Graeme, Crosswell 2001).. Sibling size hierarchy is also of major importance in hatching asynchrony where younger chicks are sometimes doomed to starvation by selfish older and much bigger chicks as seen in (Vinuela 2000). In our simulation we put this as a proportional measure (8) between the sum of chicks total weight m(i)+m(j) in relation to the contestants weight m(i)

$$pw(i, j) = \frac{m(i)}{m(i) + m(j)} \quad (8)$$

Larger chicks will have a natural size advantage to minors in proportion pw(i,j) (8). Using the probability measure as input to our stochastic process we rank each chick accordingly to winnings or loss for each game. Rankings are later used to determine most dominant chick upon the event of feeding.

Probability for ranking as most dominant (9) is determined by the dominant chicks ranking in relation to the remaining chicks within the same brood. Rankings are always set at a bias level in the beginning of the simulation. Bias is needed to insure non-negative ranking values due to increased loss.

$$pdom(i,j) = \frac{r(i)}{r(i)+r(j)} \tag{9}$$

If stochastic process for determining domination gives advantage to chick (i) in both cases {chick A-Chick B} and {Chick A-Chick C} then chick (i) will win domination game and get the best position for next feeding round. If no chick is winning more than one domination game the chick with the highest ranking will be ranked as dominant.

# 4 RESULTS

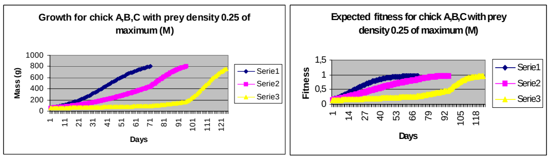
## 4.1 Evaluation of Parkers optimisation algorithm for inclusive fitness

The purpose of the first test aims to show how food is distributed by the dominant chick holding the criteria for maximization of inclusive fitness. When the first dominating chick is leaving for fledging the simulation shifts from three sib co-operation to two sib co-operation.

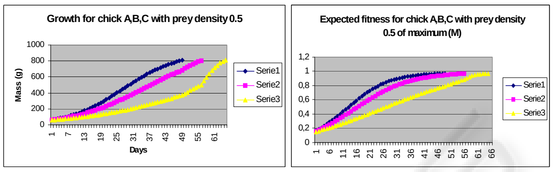
Treshold for fledging is set to 800 grams. Initial weight for each chick is 50 grams. The time scale represents the number of days within the nest until fledging. Domination stays the same throughout the whole test. Chick A is dominating food distribution from start. Simulation were performed with altered prey density. Graph 4.1.1 shows growth and fitness rate with prey density 0.25. Graph 4.1.2 shows growth and fitness rate with prey density 0.5.

### 4.1.1 Observations during the test

In the first test with prey density 0.25 Chick C is likely to suffer from starvation considering the slow growth rate. As expected the mass curve for chick B is much closer to A than C. However mass and fitness curves for prey intensity 0.5 shows higher increase of mass for chick C. As food abundance increase portions will be shared more equally between chicks.




Graph 4.1.1: Growth and fitness for Chick A, B, C with low prey density k= 0.25.



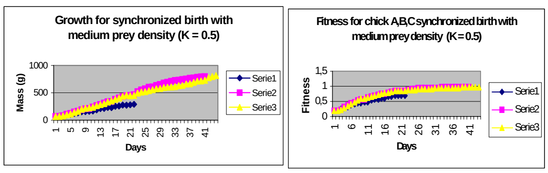

Graph 4.1.2: Growth and fitness for Chick A,B, C with medium prey density k=0.5

## 4.2 Simulating synchronized hatching with medium prey density (k=0.5)

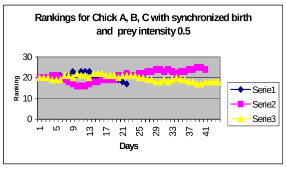
In this test algorithms for conflicting behaviours were activated which means that rankings were altered dependent on winnings through out the simulation. Shifted rankings also means that domination were altered amongst sibs during feeding. Low food abundance resulted in starvation shifting from 10-30% amongst siblings within the brood. Graph 4.2.1-Graph 4.2.2 shows mass, fitness and rankings for all three siblings. Note that deviation listed in the table represents a mean value for all deviations acquired during all ten simulations.

Table I: Synchronized hatching with medium prey density k=0.5. Running 10 simulations

| Chick | Fledging (days) | Fledged | Starved | Ranking (mean) | Ranking (dev) |
|---|---|---|---|---|---|
| A | 45.75 | 8 | 2 | 20.5 | 1.97 |
| B | 48.67 | 7 | 3 | 19.49 | 1.243 |
| C | 48.56 | 9 | 1 | 20.48 | 2.06 |




Graph 4.2.1: Growth and fitness for synchronized hatching with medium prey density k= 0.5



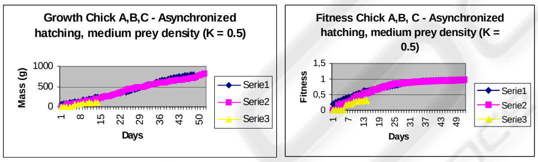

Graph 4.2.2: Rankings for synchronized hatching with prey density k=0.5

## 4.3 Simulating hatching asynchrony with medium prey density (k=0.5)

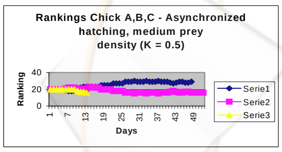
In this test each agent was activated asynchronous with a time delay of 3 tics in between each chick. In practical terms this means starting threads in Java asynchronous. Each tic corresponds to one day in a reality setting. The results shows a definite starvation for the latest hatched chick C which also has the smallest size advantage in proportion to A, B upon hatching. As expected chick A gets the highest ranking followed by B and C. Growth, fitness and rankings are shown in graph 4.3.1-4.3.2.

Table II: Hatching asynchrony with medium prey density k=0.5. Running 10 simulations

| Chick | Fledging (days) | Fledged | Starved | Rank (mean) | Ranking (deviation) |
|---|---|---|---|---|---|
| A | 46,9 | 10 | 0 | 21,28 | 2,1183 |
| B | 49,9 | 10 | 0 | 19,74 | 1,8052 |
| C | (-) | 0 | 10 | 19,50 | 0,786 |




Graph 4.3.1: Growth and fitness for hatching asynchrony with medium prey density k=0.5.



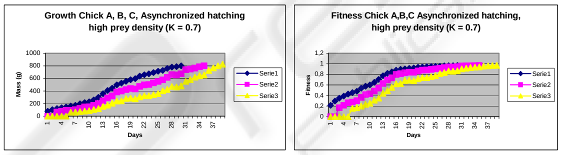

Graph 4.3.2: Rankings for hatching asynchrony with medium prey density k=0.5

## 4.4 Simulating hatching asynchrony with high prey density (k= 0.7)

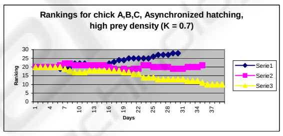
In the fourth test hatching asynchrony was performed for higher prey density 0.7. With higher food abundance all chicks reached to the state of fledging. The growth rate was also higher for all three siblings. Fledging for chick A only took 30,2 days, chick B 34,2 days and chick C 39,6 days on average. This is of course just a theoretical measure. Growth, fitness and rankings are shown in graph 4.4.1-4.4.2.

Table III: Hatching asynchrony with high prey density k=0.7. Running 10 simulations

| Chick | Fledging (days) | Fledged | Starved | Ranking (mean) | Ranking (deviation) |
|---|---|---|---|---|---|
| A | 30.2 | 10 | 0 | 21.66 | 1.514 |
| B | 34.2 | 10 | 0 | 20.31 | 1.461 |
| C | 39.6 | 10 | 0 | 17.34 | 2.197 |




Graph 4.4.1: Growth and fitness for hatching asynchrony with high prey density k=0.7




Graph 4.4.2: Rankings for hatching asynchrony with high prey density k=0.7

# 5 DISCUSSION

Mocks theory relies on the assumption that the most dominant chick controls food distribution amongst co-siblings. The theory also assumes that dominance hierarchy is fixed through out the simulation. In our simulation we have chosen to allow alterations of dominance between siblings as a result of winnings and loss. It is consistent with the results that there is a correlation between rankings and the amount of parental investment that the chick receives. In cases of simulated hatching asynchrony the latest hatched chick is likely to get a lower ranking because of the natural size hierarchy and lower chances of winning a food/dominance contest.

In a realistic setting it is likely that parents will have a greater influence in portioning food partly affected by begging patterns produced by each offspring (Kölliker 2001). Begging models needs to be considered in order to get a more accurate results for actual distribution. The influence of begging models is also a stressed in (Mock, Parker 1998) .

# 6 CONCLUSIONS

From the first simulations with three sib and two sib co-operation it follows that Mocks principles of inclusive fitness behaves as expected. When food abundance is low the chick with the lowest rank is likely to suffer from starvation. When agents were started in synchrony performed simulations shows that any chick may suffer from starvation if food resources are poor. However, when agents were started in asynchrony it is also consistent with the results that the latest hatch sibling dies due to starvation in most cases.

Our first experimental model for brood reduction has shown some interesting results that could be useful for simulation of incubation behaviours such as hatching asynchrony but of course the model needs further refinement in describing state and policy variables for each agent. Further research is needed to describe dominance/ranking and learning processes for each agent. In our simulation we have not yet considered important component of learning strategies for competition. Conflicting behaviours have a degree of learning and adaptation. Adaptation to conflicting behaviours needs to be considered if the experimental model for brood reduction should be representative for any real world situation.

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