Games among cannibals: competition to cannibalize and parent-offspring conflict lead to increased sibling cannibalism

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Abstract

Sibling cannibalism occurs in many species, yet understanding of sibling cannibalism as an adaptation currently lags behind understanding of other antagonistic interactions among siblings. Observed sibling cannibalism phenotypes likely reflect the interaction between competitive games among siblings and parent-offspring conflict. Using a game-theoretic approach, we derive optimal offspring cannibalism behaviour and parental modifiers that limit or facilitate cannibalism. The results are compared to contemporary frequency-independent analysis. With the addition of game interactions among siblings or parent-offspring co-evolution, our model predicts increased cannibalism (compared to the frequency-independent prediction), as offspring compete to eat siblings. When infertile eggs are present – strengthening competition – offspring risk eating viable siblings in order to gain access to infertile eggs, intensifying parent-offspring conflict. We use the results to make new predictions about the occurrence of sibling cannibalism. Additionally, we demonstrate the utility of trophic egg laying as a maternal mechanism to promote egg eating.

Introduction

Although there is typically a high degree of relatedness among siblings, antagonistic sibling interactions are frequently observed. Selfish sibling interactions may be broadly categorized by whether they involve competition for resources or cannibalism (Mock & Parker, 1997). As an example of resource-based competition, many nestling birds compete for limited parental investment (Mock & Parker, 1997, and refs therein). In the extreme case, there may be selection to eliminate competitors via siblicide (e.g. O’Connor, 1978). In contrast, for cannibalistic interactions, obtaining a meal (in the form of a relative) is generally the driving selective pressure. Sibling cannibalism occurs across diverse taxa, and illustrative species may be found within insects (e.g. Michaud & Grant, 2004), other invertebrates (e.g. Iida, 2003), birds (refs within Stanback & Koenig, 1992), Amphibia (refs within Crump, 1996) and fish (e.g. Fitzgerald & Whoriskey, 1992).
on a ‘simple’ optimization approach (sensu Mock et al., 1998), in which the optimal strategy (to eat a sibling or not) does not depend on the actions of other siblings in the same clutch. Yet it is clear that, when offspring interact in groups, victim siblings themselves become a resource over which cannibal siblings compete (Mock et al., 1998). Such competition may change the benefit thresholds for sibling cannibalism from the current prediction.

Furthermore, current models of sibling cannibalism do not incorporate parental interests in the degree of cannibalism among their offspring. It can be optimal for parents to facilitate or to limit selfish interactions among offspring, depending on the benefit that an offspring receives from a selfish act towards a sibling, relative to the cost of the act for the target sibling (O’Connor, 1978). Because the thresholds for parents and offspring to benefit from cannibalism differ (as described below), parent and offspring interests may overlap or conflict. Mothers have several tactics available for managing cannibalism among offspring. For example, hatching synchrony may limit sibling egg cannibalism (e.g. Frechette & Codere, 2000), whereas hatching asynchrony (e.g. Polis, 1981) and trophic egg laying (the production of infertile eggs as food for offspring, Crespi, 1992; Perry & Roitberg, 2005) facilitate egg eating.

Evolutionary games between two sets of family members – among siblings and between parents and offspring – may, then, influence observed sibling cannibalism behaviour. This study investigates the effect of these games on predicted sibling cannibalism behaviour. We model the co-evolution of sibling cannibalism and two maternal tactics – hatching synchrony or asynchrony and trophic egg production – for managing cannibalism among offspring. Given the complexity of a co-evolving, multiple-trait system, there is a large set of possible solutions. Here, we use stochastic simulation models (Goldberg, 1989) to determine the evolved outcome. In separate experiments, we investigate how three factors alter the expected frequency independent thresholds: (1) a SR game; (2) the co-evolution of, or constraints on, parent and offspring traits; and (3) infertile eggs, which were introduced to intensify the competitive game among siblings. We use the results to make new predictions about expected patterns of sibling cannibalism behaviour. The study also has implications for the evolution of trophic egg laying.

**Current understanding of sibling cannibalism**

Eickwort (1973; see also Crespi, 1992; Pfennig, 1997) used Hamilton’s rule to investigate the conditions favouring sibling cannibalism. To review the argument, consider a senior offspring (‘A’) with a probability of survival, \( P_s \), in a two-offspring clutch. If A cannibalizes its junior sibling (‘C’), it receives an increase in survival, \( P'_s \), through reduced starvation risk, and has total survival \( (P + P'_s) \). By re-stating Hamilton’s Rule (Hamilton, 1964) for the spread of a selfish act (Mock & Parker, 1997), sibling cannibalism is favoured when the relative benefit to the cannibal exceeds the cost to the victim, weighted by relatedness – that is, when \( P'_s / P_s > r \). This can be restated as

\[
P'_s / P_s > r.
\]

For example, a cannibal must increase survival by at least 50% to profit from consuming a full sibling. Throughout the paper, we refer to the term \( (P'_s / P_s) \times 100 \) as the relative benefit of cannibalism (RBC).

As mentioned above, in this model of sibling cannibalism, the optimal phenotype does not depend on the frequency distribution of phenotypes in the population. In the model, the probability of survival of the victim C, \( P_C \), is equal to the probability of survival for all offspring, \( P^* \). The optimal cannibalism behaviour of A with respect to C is then considered, using \( P^* \) as the basis of the inclusive fitness cost of eating C. However, if clutch size is increased to three and there is a second senior offspring, B, then the true value of \( P_s \) is modified by B’s phenotype: \( P_C \) now depends on the frequency distribution of phenotypes in the B offspring position. As the frequency of the cannibalistic phenotype in the population \( f \) increases, \( P_C \) approaches 0:

\[
\lim_{f \to 1} P_C = 0
\]

whereas, if cannibalistic phenotypes are rare, the approach used above becomes approximately correct:

\[
\lim_{f \to 0} P_C = P^*.
\]

It is clear, then, that when siblings interact in groups of more than two, the usual frequency independent analysis may not apply.

From a parent’s perspective, sibling cannibalism provides a net benefit when more offspring are gained from the increased survival of cannibals than are lost as victims (e.g. Crespi, 1992). With pairwise sibling interactions, this occurs when

\[
P'_s > P_s.
\]

Parents favour cannibalism when the survival of cannibals is at least doubled through cannibalism (when RBC > unity).

The model demonstrates that parent and offspring interests may overlap or conflict, depending on intra-clutch relatedness and the relative increase in survival from cannibalism. Neither parents nor offspring benefit from cannibalism when RBC < r. When \( r < RBC < 1 \), it is in the interests of offspring to cannibalize siblings and the interests of parents to prevent cannibalism. When RBC > 1, parents and offspring agree that cannibalism should proceed. The model also shows that, for sibling cannibalism to be beneficial, a noncannibal’s probability...
of survival must be low. For example, if \( P > 2/3 \), individuals cannot be selected to eat full siblings due to the constraint that \((P' + P) \leq 1\). Similarly, for parents to favour sibling cannibalism survival must be less than 50%, else eqn 2 cannot be satisfied.

The models

In computer simulations, we modelled sibling egg cannibalism and maternal influence of cannibalism over many generations, allowing coded ‘genes’ for the behaviours to evolve according to the success of the coded strategy. To describe the ecological situation of interest in general terms, we consider sibling interactions within clutches of more than two offspring, with potential egg cannibalism, no parental care, and dispersal of offspring after egg cannibalism. Within a clutch, we assume that offspring hatch more or less synchronously, with the degree of synchrony under maternal control. We assume that cannibal offspring consume, at most, one egg. Cannibals may consume a potentially viable sibling, or an infertile or trophic egg. Infertile eggs are produced by constraint (i.e. mothers cannot avoid producing them), whereas trophic eggs are produced according to a mother’s trophic egg gene. We assume that viable, infertile and trophic eggs provide equal food value. We assume that cannibals do not discriminate between viable and inviable eggs; there is apparently no such discrimination in several well-studied empirical systems (e.g. Pienkowski, 1965; Baur & Baur, 1986). Mothers produce only one clutch, after mating once.

In our simulations, individuals were represented as 12-byte strings of information, divided into 4-byte segments (here, genes) that code for the hatching synchrony, trophic egg laying, and cannibalism lag time behaviours. Each individual possessed all three genes, with the cannibalism gene expressed in offspring and the hatching synchrony and trophic egg genes expressed in mothers.

In interactions within clutches, each pair of haploid parents produces one clutch of 16. The number of trophic eggs (0–15) is determined by the mother’s trophic egg allele; ‘trophic’ status is assigned randomly. The remaining viable offspring hatch over 16 time units, in a pattern determined by the mother’s allele for hatching synchrony (Table 1). For example, all offspring might hatch within one time unit, or hatching might be spread out over time. In each time unit, the hatching offspring (if any) was selected randomly. After an offspring hatches, it waits some number of time units (1–16, determined by its allele for ‘cannibalism lag time’) before seeking an egg to eat within its clutch; victims were selected randomly from remaining unhatched eggs. A delay of 16 time units permits all viable siblings to emerge. After time 16, offspring may continue to consume any trophic or infertile eggs present (to a maximum of one egg per offspring). Thus, an offspring’s opportunity to cannibalize depends on the availability of unhatched eggs when it emerges and the combination of its hatch time and delay time. For example, an offspring that hatches at time 5 and has a lag time of 12 will seek an egg to eat at time 17, when all potentially viable eggs will have hatched.

Table 1 The range of hatching synchrony phenotypes tested in simulations, expressed as the number of offspring that hatch in each time period. Mothers produce clutches with the hatching pattern indicated, based on the allele they possess.

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Blank cells signify zeroes.

*Derived for a clutch size of 16 and the condition that offspring eat, at most, one egg. Alleles closer to 16 allow maximal cannibalism at a wider range of offspring cannibalism delay phenotypes.
For each generation, interactions within two hundred clutches were simulated simultaneously and independently. When time ended (i.e. when no further hatching or egg eating could occur within a clutch), successfully hatched offspring had a probability of surviving starvation that was dependent on number of eggs consumed (0 or 1). From the survivors, 200 pairs of individuals were randomly selected as parents of the next generation. Thus, fitness was assigned indirectly: successful alleles made more copies of themselves and were proportionally more represented in the pool from which reproducing individuals were drawn.

The algorithm that we used, often referred to as a genetic algorithm, introduced new alleles – from which to search for optimal strategies – through mutation- and crossover-like processes during reproduction. The chance of mutation (i.e. changing a 1 to 0 or 0 to 1) was 1% at each byte locus. When crossover occurred (in 10% of offspring) the parental chromosomes were spliced at a random location anywhere along the string. High rates are used to quickly generate the variation from which optimal solutions may be found (as in, e.g. Browning & Colman, 2004). For some simulation sets, we conducted replicates with mutation and crossover (MC) rates set to 0 to ensure that the introduction of new alleles did not influence the results. By incorporating these two natural selection-like processes – differential success of inherited traits and the testing and re-testing of strategies through the introduction of new alleles – the algorithm finds the evolutionarily optimal phenotype for each behaviour considered. Because genetic algorithms can quickly search a large strategy set, they are a valuable technique for complex co-evolutionary games (e.g. Forrest, 1993).

To initialize simulations, a population of 400 randomly drawn strategies was created (i.e. the aforementioned 12-byte strings). For each parameter set examined, we conducted five simulation runs with different random number seeds. Simulations ran for 1000 generations; gene values stabilized after approximately 100 generations.

Control simulations: frequency independence
In a set of control simulations, we tested that our model reached the same conclusions as the frequency-independent model (outlined in the introduction) when the assumptions were identical.

First, we tested the cannibalism lag time gene when competition among cannibals was prevented, there was no parent-offspring co-evolution and no happenstance infertile eggs. To prevent the SR game, we randomly paired offspring at the beginning of within-clutch interactions. The first-hatching offspring within each pair could consume only the egg it was paired with; if the paired egg was not consumed, no other offspring was permitted to eat it. To prevent parent-offspring co-evolution, we permitted only one gene to evolve per simulation set. The other genes were fixed for one allele value in all individuals, and mutation was prevented within these genes. In these simulations, the cannibalism lag time gene evolved, while trophic egg laying was prevented and hatching was maximally asynchronous. Thus, offspring could potentially consume viable siblings, creating selection on the cannibalism lag time gene, with the direction of selection pressure dependent on the RBC value.

Next, we tested the two maternal genes when parent-offspring co-evolution was prevented and there were no infertile eggs. In the second set of control simulations, we allowed hatching synchrony to evolve with cannibalism lag time fixed at minimal (creating selection on mothers to manage cannibalism among their offspring) and trophic egg laying prevented (constraining them to respond with hatching synchrony alone). Finally, we allowed the trophic egg gene to evolve with cannibalism lag time fixed at minimal and hatching at completely synchronous. In these simulations, mothers could not prevent sibling cannibalism, but could facilitate egg laying by laying trophic eggs.

After confirming that our simulations could generate the frequency-independent predictions for optimal offspring and maternal behaviours, we conducted three experiments (described below) that introduced game interactions, parent-offspring co-evolution, and intensified competition. We compared the predicted evolutionarily stable mean phenotypes from these models to those of the controls.

Experiment 1: a sibling rivalry game
To introduce SR, eggs were not paired as described above. Any hatched offspring could consume any unhatched egg. To ensure that the introduction of variability through MC did not affect the results, we ran simulations with MC rates set to 1 and 10%, respectively, or to 0%. The response variable of interest was the optimal cannibalism lag time. We compared the optimal lag time from these simulations to the first set of control simulations, in which the competitive game among siblings was prevented. As in the first set of control simulations, both maternal genes were fixed, with hatching at maximally asynchronous and trophic egg laying prevented.

In further simulations, we permitted either the hatching synchrony or trophic egg laying genes to evolve with the other genes fixed (as described for the second set of control simulations) and with competitive interactions among offspring. These simulations are used for comparison with experiment 2.

Experiment 2: parent-offspring co-evolution
Parent-offspring co-evolution was introduced by permitting all three genes to evolve at once. We tested whether co-evolution affected the optimal maternal and offspring phenotypes by comparing the results of these simulations
to those of experiment 1, in which a competitive game among siblings was present but co-evolution was prevented.

**Experiment 3: happenstance infertile eggs**

We introduced happenstance infertile eggs (i.e. unavoidable infertility, in contrast to trophic eggs under a mother’s genetic control) to intensify the competitive game among siblings. Simulations were conducted in which all clutches contain such eggs (2 per clutch of 16), and in which SR and co-evolution were also present. We tested the effect of infertile eggs on optimal maternal and offspring traits, compared to the optimal phenotypes from experiment 2. In these (and all) simulations, offspring could consume infertile eggs after all viable siblings hatched, if lag times were long enough.

**Statistical analyses**

We took the evolutionarily stable mean phenotypes to be the mean allele value of each gene for the last 200 generations, averaged over all individuals in the parent population and taken every 10th generation. Allele values and phenotypes correspond: the cannibalism lag time allele represents the average number of time units that offspring wait before attempting to eat an egg; the trophic egg allele equals the number of trophic eggs in a clutch; and the hatching synchrony allele corresponds to the hatching patterns in Table 1. To test for an effect of treatment (in experiment 1, presence or absence of competition among siblings; in experiment 2, presence or absence of co-evolution; in experiment 3, presence or absence of infertile eggs), we included the factors RBC, treatment, and the RBC × treatment interaction in ANOVA models using the program JMP 5.0. In experiment 1, the additional factor of ‘MC’ – prevented or allowed – was included, along with two-way interactions (the three-way interaction term was not significant and was therefore dropped from the final model). The response variables were the evolutionarily stable mean phenotypes for the responding genes (for experiment 1, cannibalism lag time; for experiments 2 and 3, all three genes). We used the Tukey–Kramer post hoc tests to test for differences between groups. Least-squares means, which account for variation in the response variable caused by all other factors in the ANOVA model, are presented.

**Results**

The results from control simulations, in which competition among potential cannibals was prevented, match the frequency independent prediction. As expected from eqn 1, when there was no competition among offspring, the evolutionarily stable cannibalism lag time declined sharply and significantly at RBC values above 50% (Fig. 1). The maternal genes of hatching synchrony and trophic egg laying also show different trajectories below and above the 100% RBC threshold (eqn 2) for mothers to benefit from cannibalism among offspring. At RBC < 100%, mothers limit cannibalism with synchronous hatching (Fig. 2b). When RBC > 100%, mothers facilitate egg consumption with asynchronous hatching (Fig. 2b) or trophic eggs (Fig. 2c).

**Experiment 1: sibling rivalry**

The addition of game interactions significantly decreased the RBC threshold at which sibling cannibalism was favoured (Table 2 and Fig. 1). With the addition of game interactions, average cannibalism lag times decreased (compared to control simulations) at 40 and 44% RBC – before the 50% threshold predicted by the frequency-independent analysis. Importantly, the interaction between RBC and game interactions was significant (Table 2): the effect of SR occurred only at 40–50% RBC (Fig. 1). At RBC values above the 50% threshold,
cannibalism lag times were minimal with and without game interactions, as predicted by both models.

Whether MC rates were set to zero or to positive values (mentioned under ‘The Models’) did not affect the evolutionary stable cannibalism lag time (Table 2). However, MC rates, in interaction with the factors RBC and game interactions, affected the evolved cannibalism lag time (Table 2). This occurred because, without MC, new alleles were not reintroduced each generation; if a particular allele became fixed, it remained fixed for the rest of the simulation.

**Experiment 2: co-evolution vs. constraints on traits**

Whether maternal and offspring traits co-evolved, or evolved independently while other traits were fixed, significantly affected the evolutionarily stable behaviours for both mothers and offspring (Fig. 2).

Co-evolution of parent and offspring traits caused a decreased average cannibalism lag time, compared to the result when only cannibalism delay evolved (Fig. 2a; $F_{1,56} = 97.5, P < 0.0001$). The decrease in lag time was significantly different at 25 and 50% RBC only, though lag time was always lower when co-evolution occurred (Fig. 2a; RBC × co-evolution interaction: $F_{6,56} = 57.0, P < 0.0001$).

The effect of parent-offspring co-evolution on hatching synchrony depended on the RBC value (Fig. 2b; effect of co-evolution: $F_{1,64} = 18.9, P < 0.01$; RBC × co-evolution interaction: $F_{7,64} = 143.5, P < 0.0001$). At 0% RBC, the effect parent-offspring co-evolution on optimal maternal and offspring phenotypes that influence sibling cannibalism. Co-evolution was permitted by allowing both parent and offspring genes to evolve (open squares), or prevented by having each trait evolve alone (filled circles) as described in the text. Of interest is the change in optimal phenotype as the relative benefit of cannibalism (RBC; see the caption for Fig. 1). Asterisks indicate significant differences among means ($P < 0.05$) by Tukey post hoc tests. (a) Optimal cannibalism lag time for offspring; longer delays indicate less willingness to cannibalize viable siblings (see text). (b) Hatching synchrony phenotypes are given in Table 1. Low values indicate more synchronous hatching and, thus, an attempt to prevent cannibalism among offspring. (c) Values for the trophic egg phenotype correspond to the optimal number of trophic eggs produced in a clutch of 16. It was never optimal to produce more than eight trophic eggs, because offspring could consume one egg at most. The factor ‘co-evolution’ significantly affected optimal phenotypes for all three behaviours ($P < 0.01$; see text). Optimal phenotypes were calculated as described in the caption of Fig. 1. Least-squares means are presented, which control for variation in optimal phenotypes caused by the RBC and the RBC × co-evolution interaction.

![Table 2](image)

**Table 2** The effect of the RBC (at levels 0–125%), sibling rivalry (SR) (present or absent), and mutation and crossover (MC) (rates set to 0 or 1 and 10%, respectively) on the average cannibalism delay gene values derived from simulations.

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<th>F Ratio</th>
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<td>&lt;0.0001</td>
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<tr>
<td>RBC × MC</td>
<td>10</td>
<td>19.1</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>SR × MC</td>
<td>1</td>
<td>6.7</td>
<td>0.0107</td>
</tr>
</tbody>
</table>

Whole model: $F_{33,186} = 138.7, P < 0.0001$. 

![Fig. 2](image)
hatching was, on average, less synchronous when co-evolution with offspring occurred (Fig. 2b). A likely explanation is that, when cannibalism lag times could evolve, lag times quickly increased to avoid sibling cannibalism at 0% RBC; hence mothers did not need to prevent sibling cannibalism with synchronous hatching. When RBC = 150%, hatching was, on average, more synchronous with co-evolution (Fig. 2b), indicating that mothers did not attempt to facilitate as much sibling cannibalism with co-evolution.

More trophic eggs were produced when the trophic egg-laying gene evolved alone, compared to the co-evolution simulations ($F_{1,72} = 37.1, P < 0.0001$); the difference was significant for RBC values of 125 and 150% (Fig. 2c; RBC × co-evolution interaction: $F_{8,72} = 46.6, P < 0.0001$). The opposite pattern occurred at 75% RBC; then the trophic egg allele was higher when co-evolution occurred.

**Experiment 3: nonevolved infertile eggs**

When we strengthened the competitive game among siblings by introducing infertile eggs, offspring became more willing to risk cannibalizing viable siblings. The average cannibalism lag time decreased significantly (Fig. 3a; $F_{1,80} = 10.2, P = 0.002$), compared to results from experiment 2 in which game interactions occurred without infertile eggs. The difference was detectable at 10% RBC (Fig. 3a; RBC × infertile eggs interaction: $F_{9,80} = 4.8, P < 0.0001$). At RBC values above 50%, the delay until cannibalism was minimal in the presence and absence of infertile eggs.

Mothers produced more synchronously hatching clutches when infertile eggs were present (Fig. 3b; $F_{1,80} = 6.8, P < 0.05$). The difference in synchrony in the presence and absence of infertile eggs was not detectable at any RBC level (Fig. 3b), though the interaction term was significant (RBC × infertile eggs interaction: $F_{9,80} = 3.0, P < 0.01$).

Unsurprisingly, fewer trophic eggs were produced in the presence of infertile eggs (Fig. 3c; $F_{1,80} = 133.4, P < 0.0001$). The difference was detectable at RBC values from 75 to 125% (Fig. 3c; RBC × infertile eggs interaction: $F_{9,80} = 5.6, P < 0.0001$).

**Discussion**

Our results indicate that games among family interactors affect both the extent of selfishness expected among siblings and parental attempts to facilitate or limit selfish interactions among offspring. We have elaborated on the
usual predictions of optimal cannibalism behaviour towards siblings, which are derived for the frequency-independent case. Below, we discuss our predicted optimal behaviours in parents and offspring (especially where these differ from frequency-independent predictions) and, where possible, compare our qualitative predictions with natural systems. The results of the model are directly applicable to species in which offspring interact within a confined physical space (a nursery, sense Mock & Forbes, 1995) for some small portion of their lives – small because extended interactions likely involve resource-based competition and, thus, an additional selection pressure favouring siblicide. Our results apply when clutch size exceeds two, and when there is the possibility of competition among siblings for cannibalism opportunities (i.e. at least two offspring are capable of eating a third); when these conditions do not exist, the frequency-independent prediction likely applies. Furthermore, our results may be extended to any selfish acts among family members in which the benefit of selfishness accrues to one individual only, such that individuals may compete to reap that benefit.

Previous predictions of the threshold for benefit from cannibalizing a sibling (Eickwort, 1973; Crespi, 1992; Dong & Polis, 1992; Pfennig, 1997) considered the frequency-independent case. Incorporating game interactions among siblings – a competition for the resource of consumable eggs – decreases the predicted benefit threshold (Fig. 1). Sibling games appear to drive the evolution of higher cannibalistic tendency than would otherwise be optimal.

A second evolutionary game – parent-offspring conflict over sibling cannibalism – also affected optimal maternal and offspring behaviours. Cannibalism lag time was reduced in simulations in which parental and offspring behaviours co-evolved (Fig. 2a), compared to simulations in which maternal traits were constrained (i.e. mothers could not prevent cannibalism with synchronous hatching, nor facilitate egg eating with asynchronous hatching and trophic eggs). A possible explanation is that co-evolution intensified the SR game. When maternal genes were permitted to evolve along with cannibalism lag time, hatching became synchronous at RBC values less than 50% – perhaps strengthening competition for rare cannibalism opportunities. In effect, maternal attempts to limit cannibalism among offspring may intensify their cannibalistic tendencies. An alternative explanation is that, with the reduced opportunity for cannibalism due to synchronous hatching (at RBC < 50%), selection against sibling-eating individuals may have weakened. However, this second hypothesis is not supported by the results: in the co-evolution simulations of experiment 2, at RBC values of 25 and 50%, cannibalism lag times decreased from the random initialization average of 7.5 time units. This pattern indicates strong directional selection, rather than weakened selection and drift.

The effect of co-evolution on hatching synchrony and trophic egg production – decreasing synchrony and trophic egg production at RBC values exceeding 100% (Fig. 3b, c) – is easily understood. At RBC > 100%, when both maternal genes were permitted to evolve, mothers used a combination of asynchronous hatching and trophic eggs to facilitate egg eating among offspring. More particularly to our next argument, mothers did not use hatching asynchrony alone. It may seem counterintuitive that a mother’s best option is to produce a trophic egg (e.g. Dixon, 2000), when instead, she could increase hatch asynchrony so that eggs may continue development if they escape cannibalism. In our simulations, it was not, in fact, better to increase hatching asynchrony than to produce trophic eggs. We suggest that mothers produce trophic eggs in order to ensure that egg eating occurs. If hatching asynchrony alone is used, there is some chance that delayed-hatch eggs will hatch first.

The control and experiment 1 simulations – in which some traits were prevented from evolving – may be similar to natural systems in which offspring or parental traits are constrained. For example, in predatory insects, offspring may experience strong selection for early predatory ability. Genetic correlations may prevent selection from separating the behaviours of attacking prey and cannibalizing siblings soon after emergence. Furthermore, mothers may be unable to make hatching perfectly synchronous, if egg formation and deposition are not perfectly precise processes. The presence of constraints gives control of the occurrence of sibling cannibalism to the unconstrained party. Thus, in natural systems, the observation of sibling cannibalism does not imply that parents experience a net fitness benefit from cannibalism; they may simply be unable to prevent it.

**Empirical predictions**

The results allow several predictions about patterns of sibling cannibalism in natural systems. First, a key prediction from the model is that, when there is competition among cannibals for victims, sibling cannibalism should occur when the RBC is less than 50%; the precise threshold favouring sibling cannibalism should depend on the strength of competition among cannibals. In contrast, the frequency independent model (outlined in the introduction) predicts sibling cannibalism only at RBC > r, the coefficient of relatedness. Testing this prediction requires quantitative estimates of the increase in survival from eating a sibling, relative to survival probability under normal food conditions without cannibalism. Most useful would be systems in which the RBC < relatedness among siblings. However, most observations of sibling cannibalism are qualitative (e.g. Byrne, 1996; Frechette & Coderre, 2000; Rienks, 2000; Margalida et al., 2004). We know of six quantitative studies of sibling cannibalism (Table 3). Of these, RBC
values less than 50% were reported for three species. For the ladybird beetle Harmonia axyridis, RBC depended strongly on local food conditions (Osawa, 1992); it is not possible to estimate an overall RBC without knowledge of how frequently individuals encounter different food environments. Ng (1986) reports RBC values of less than 50% for two other ladybirds, Coleomegilla maculata lengi (25%) and Spilocaria bisellata (37%; Table 3), in which sibling cannibalism is common. Average relatedness in these species is not known; the possibility that offspring are less than full siblings cannot be excluded. However, this study measured the benefit of cannibalism relative to ‘no food’ conditions, and thus overestimates the RBC experience in natural conditions. Given that offspring within a clutch have relatedness of 0.25, cannibal C. maculata lengi apparently experience an RBC value less than relatedness among siblings. Hence, the pattern is consistent with the hypothesis that game interactions drive the evolution of increased tendency to cannibalize siblings, but not with the frequency-independent hypothesis that offspring should cannibalize full siblings only if RBC > 50%. Additional studies quantifying RBC values compared to natural conditions would be of great interest in light of this prediction. Studies of related taxa in which some species exhibited sibling cannibalism and others did not (e.g. coccinellids) would be especially useful, if noncannibal species could be induced to consume siblings so that the benefit of doing so may be measured.

A second and related prediction is that sibling cannibalism should be more common in species with game interactions among siblings, compared to species in which there is no game. Sibling cannibalism should, then, be more common in species that produce clutches of two or more offspring, compared to species in which clutch size is two. The prediction is difficult to test with a particular taxonomic group. For example, few insect taxa produce clutches of only two eggs. While two-egg clutches are more common in birds, bird nestlings experience strong resource competition, and cannibalism in birds is probably driven by the need to eliminate a competitor rather than the value of siblings as meals (Fitzgerald & Whoriskey, 1992).

In our model, the presence of infertile eggs strengthened the competitive game among siblings, further lowering the RBC threshold for sibling cannibalism (Fig. 3a). In the model, cannibal offspring had the option of waiting until viable siblings had hatched before consuming infertile eggs; instead, cannibals risked eating viable siblings to gain access to infertile eggs first. Thus, a third prediction is that sibling cannibalism should occur more frequently in species that produce infertile eggs, if, as assumed in our model, offspring cannot distinguish between viable and infertile eggs. This prediction is complicated by the possibility that infertile egg production is under maternal control – i.e. that the infertile eggs are trophic eggs. Trophic eggs are expected only when RBC > 100%, that is, when sibling cannibalism is favoured even without game interactions. Thus, in testing this prediction, it will be important to distinguish infertile eggs produced by constraint from infertile eggs that serve a trophic function. The presence of infertile eggs – common in many taxa – has implications for sibling cannibalism because it strengthens competition among siblings.

Table 3 Quantitative studies of sibling cannibalism. The RBC refers to the increase in survival that cannibals experienced, relative to survival without cannibalism in the food conditions indicated.

<table>
<thead>
<tr>
<th>Species</th>
<th>RBC (%)</th>
<th>Comparison</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coccinellidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Harmonia axyridis</td>
<td>16</td>
<td>Noncannibals at high aphid (prey) density</td>
<td>Osawa (1992)</td>
</tr>
<tr>
<td>Harmonia axyridis</td>
<td>226</td>
<td>Noncannibals at low aphid (prey) density</td>
<td>Osawa (1992)</td>
</tr>
<tr>
<td>H. axyridis</td>
<td>114</td>
<td>Unfed larvae with access to water</td>
<td>Kawai (1978)</td>
</tr>
<tr>
<td>C. maculata lengi</td>
<td>25</td>
<td>Unfed larvae without water</td>
<td>Pienkowski (1965)</td>
</tr>
<tr>
<td>S. bisellata</td>
<td>37</td>
<td>Unfed larvae without water</td>
<td>Ng (1986)</td>
</tr>
<tr>
<td>Menochilus sexmaculatus</td>
<td>70</td>
<td>Unfed larvae without water</td>
<td>Ng (1986)</td>
</tr>
<tr>
<td>Coleomegilla inaequalis</td>
<td>84</td>
<td>Unfed larvae without water</td>
<td>Ng (1986)</td>
</tr>
<tr>
<td>Coccinella repanda</td>
<td>135</td>
<td>Unfed larvae without water</td>
<td>Ng (1986)</td>
</tr>
<tr>
<td>Other taxa</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Admerus triguttulus</td>
<td></td>
<td></td>
<td>Baur (1990)</td>
</tr>
</tbody>
</table>

Conclusion

Because sibling cannibalism is found in many diverse taxa, it is important to understand the selective forces driving its evolution. Previous understanding of sibling cannibalism is summarized by Mock & Parker (1997), p. 6: ‘when a sib is more valuable as food than as a gene bearer, it should be consumed’. We may now add to this condition, ‘it should also be consumed if it will be consumed by another sibling anyway’. Mock & Parker (1997) highlighted the potential importance, and deficit of study, of evolutionary games within family units for
the evolution of selfishness among siblings. Our results demonstrate that game interactions can indeed contribute new insights to predictions of optimal behaviour for family members. Moreover, considering such interactions in a framework of negotiated change leads to new insights compared to a static optimality approach (McNamara et al., 1999). There is clearly scope for further work in modelling how other factors – for example, offspring potential to consume more than one egg, or to discriminate between viable and infertile eggs – change predictions for optimal behaviour of family members towards each other.

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