The role of collective reproduction in evolution

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Abstract. To look for an answer to the puzzle of why complexity may increase, this paper looks to the major evolutionary transitions – a recurring pattern where individuals give up their rights to reproduce individually and instead reproduce as part of a super-organism. A simple model of collective reproduction is presented and discussed in light of this topic. The model finds that collective reproduction is actually to the benefit of the individual, not to the group. The cost of reproduction is shown to be an important factor and different scenarios are presented which show individual, sexual reproduction and collective reproduction (with larger numbers of parents) as optimal.

1   Introduction

One of the most striking features of our evolutionary past is the rise of the complex individual. As we replay the timeline of natural history [1], the most complex species has become increasingly more complex. One of the major goals of Artificial life has therefore been to recreate such increases in individual complexity *in-silico* [2]: i.e., within a computer.

The common opinion in biological circles [3] is that core evolutionary theory is all we need to explain the evolution of life and its astounding complexities. However, this does not seem so hopeful when attempts to reproduce such effects in ALife computer models, which implement all the main features of evolutionary theory, have not produced much complexity of interest whatsoever [4]. It seems clear therefore that there is something missing, perhaps just from the models that have attempted to recreate some of the complexity of life, or perhaps even from the evolutionary theory they are based on. This paper looks for a process (or processes) that can increase the complexity of an individual.

A profound theme observed in nature is the hierarchical structures (units made up from sub-units) that can be found [1]. These hierarchical structures are a recurring pattern, and can be seen at all levels of biology. The important feature at every level of these hierarchies is that units are made up of sub-units: proteins are made of chains of amino acids, cells/organelles are made of proteins, eukaryotic cells are made up of organelles, multicellular organisms are made up of eukaryotic cells, and societies are made up of multicellular organisms. Each unit is of greater complexity than each sub-unit.

This repeating pattern implies that there may be some common feature in individual sub-units from every level that leads them to form themselves into

larger units: an evolutionary force that binds these units together. Or, put another way, a mode of interraction that is common to sub-units at every level. In fact, these sub-units have common features at every level. They all make copies of themselves, which may or may not be perfect copies, and they all compete with other similar individuals over resources.

One other feature has been highlighted and is seen in the literature studying the evolution of new super-units from sub-units. These evolutionary steps have been dubbed *major evolutionary transitions* [1]. It has been observed that all of the transitions are characterised by one simple common paradigm: sub-units that could previously reproduce on their own can now only reproduce as part of the super-unit [5]. Since each of the transitions involves an increase in individual complexity, I look for a general model of the transitions which can illuminate processes for increase in individual complexity.

A common approach to explaining some of the individual transitions is to look to altruism and social evolution. The central thesis, here, is that any individual involved in collective reproduction is performing an altruistic act. I.e., taking a reduction in their own reproductive success so that the reproductive success of the group may increase. It has long been rejected that an individual may reduce its fitness (lifetime reproductive success) to benefit its local group [6]. However, it has been shown how an individual may take a reduction in personal fitness to benefit related organisms [7, 8] through *kin selection*.

The kin selection perspective has shown some value in explaining the maintenance of eusociality (social insects), however it is not clear that it (or altruism in general) explains the origins of this transition [1, 9]. Indeed one problem with kin selection is that its benefits can be negated by increased local competition for food [10]. One question, considered here, is therefore whether altruism actually is crucial for explaining the origins of collective reproduction. It may be possible to find explanations that are mutualistic: i.e., the outcome for both the individual and the group is beneficial.

On the face of it, given the literature on the cost of sex (e.g., [11, 12]), it looks unlikely that a mutualistic explanation may be found for collective reproduction. Put simply, the cost of sex means that individuals which reproduce sexually will grow at a slower rate than those that reproduce individually. Rather than directly considering Maynard Smith's model of the cost of sex, I illustrate the problem by reformulating it within the abstract terms used in this paper. Here, I make a simple comparison of the growth rates of an individual strategy and a collective reproduction strategy (with two parents) based on the way resources are allocated to offspring, as shown in Fig. 1.

Since individuals with the collective strategy share contributions to offspring, they contribute less than those with the individual strategy. This means that the average level of resources per individual in the collectively reproducing population will be higher than those in the individually reproducing population. For a fixed input of resources to the system, this means that the collectively reproducing population will grow more slowly than the individually reproducing population. If we look at cases where there are increasingly larger numbers of
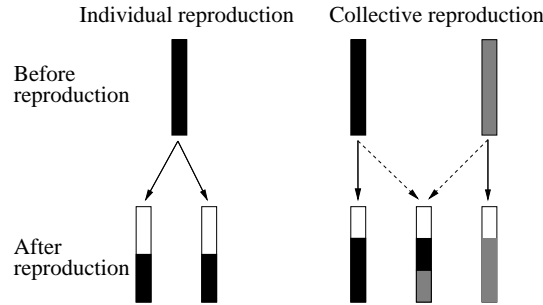
Fig. 1. Individual reproducers will grow more quickly than collective reproducers. Individuals are represented as resource containers of size R_1, with the level of resources represented by how full the containers are. They are shown just before, and immediately after reproduction. Each new individual from the sexually reproducing population will have an average resource level of $2R_1/3$ so, for the same resource input, this population will grow more slowly than the individually reproduction population which starts with an average resource level of $R_1/2$.

parents, then the same reasoning can be used to show that the growth rate will be increasingly slower (e.g., when there are 3 parents, this population will have an average resource level of $3R_1/4$ after reproduction).

Given this cost of collective reproduction, it seems unlikely that there is any advantage to collective reproduction. However, this analysis only looks at the growth phase. Any population that grows will eventually exhaust the resources in its environment and the population will either decline or reach a static level. Because collectively reproducing individuals have, on average, greater resources after reproduction they are less vulnerable during times of population decline.

To approach modelling the major evolutionary transitions, I take an abstract perspective in order to produce a toy model. This approach, based on the common factors of the subunits identified above, simplifies the world to resources, individuals and individual strategies. Individuals accumulate resources, expend resources, make copies of themselves and share resources with those copies. Given that an individual lives within an environment with factors outside of its control, I assume that they have little control over the way they accumulate or expend resources. The space of strategies that they may adopt is therefore concerned with their reproduction strategy.

The model simply approaches the question as to whether it is a better strategy, for the individual, to reproduce collectively or to reproduce individually. It is looking for an explanation for collective reproduction that is not based on altruism. In the next section I present the model and its results.

2 The model

Two modelling approaches are taken in this section. After presenting details common to both approaches, I outline a mathematical model and its predictions.

The predictions of the mathematical model are tested by simulation models in Section 2.2.

Here each individual i is modelled as a resource level $x(i, t)$ by the equation,

$$x(i, t + \delta t) = x(i, t) + u(t)R_u - R_c \ , \tag{1}$$

where δt, R_u and R_c $[0 < R_c < R_u]$ are positive constants (R_u is the maximum resources available for uptake and R_c is the cost of growth/maintenance each timestep of length δt). *Resource uptake* (the level of resources received from the environment) is variable and modelled by $u(t) \in [0 : 1]$. The variable u here is used as a surrogate for competition: population fluctuations will lead to increasing and declining phases, modelled by changes in the behaviour of u.

If an individual's resource level decreases below the lower threshold R_0 (fixed for all individuals) it will die. Without losing generality, R_0 is set to 0 as an *ad hoc* simplification. If an individual's resource level increases above the reproduction threshold (R_1) it will reproduce. All individuals pay a cost of reproduction $R_r(n)$ which is dependent on the number of parents n.

2.1 Mathematical treatment

The mathematical treatment assumes that u is static over the lifetime of individuals. The resource change δx over a discrete time interval δt is therefore modelled as:

$$\delta x = u R_u - R_c \ . \tag{2}$$

The value of u where $\delta x = 0$ is defined as u_0: $u_0 = R_c/R_u$.

During reproduction all parents pay the cost of reproduction $R_r(n)$. After this the remaining resources are shared equally between the n parents and the offspring. All individuals therefore start their lives, just after reproduction, with $x = n(R_1 - R_r)/(n + 1)$. Two cases for u can now be considered: $u > u_0$ and $u < u_0$. In the first case the individual resource level will increase until it reaches the upper threshold R_1, taking an expected time W where,

$$\begin{aligned} W_{u > u_0} &= \left[R_1 - \frac{n\,(R_1 - R_r)}{n + 1} \right] \frac{\delta t}{\delta x} \\ &= \frac{(R_1 + nR_r)\,\delta t}{(n + 1)\delta x} \ . \end{aligned} \tag{3}$$

In the second case individual resources will decrease until it reaches the lower threshold at resource level R_0. The expected time W is,

$$W_{u < u_0} = \frac{n\,(R_1 - R_r)\,\delta t}{(n + 1)\delta x} \ . \tag{4}$$

In both cases, as $u \to u_0, W \to \infty$.

The expected population growth rate of a homogeneous population of individuals can be estimated for the two regimes ($u > u_0$ and $u < u_0$). The

expected population growth rate per individual G is equal to the reciprocal of the time taken for resources to grow for reproduction during population growth $(1/W_{u>u_0})$ and reciprocal of the time taken for resources to decline for death during population decline $(1/W_{u<u_0})$, or [substituting Equation (2) into Equations (3) and (4)]:

$$G = \begin{cases} \dfrac{(n+1)(uR_{\mathrm{u}} - R_{\mathrm{c}})}{n\left(R_1 + nR_{\mathrm{r}}\right)\delta t} & , u > u_0 \\[2ex] 0 & , u = u_0 \\[2ex] \dfrac{(n+1)(uR_{\mathrm{u}} - R_{\mathrm{c}})}{n\left(R_1 - R_{\mathrm{r}}\right)\delta t} & , u < u_0 \,. \end{cases} \tag{5}$$

The growth rate (G) is plotted against different values of u for one $[n = 1,\ R_{\mathrm{r}}(1) = 0.1]$ and two $[n = 2,\ R_{\mathrm{r}}(2) = 0.05]$ parents in Fig. 2. In this case, the two parents share the cost of reproduction born by the single parent – i.e., the cost per offspring is the same.
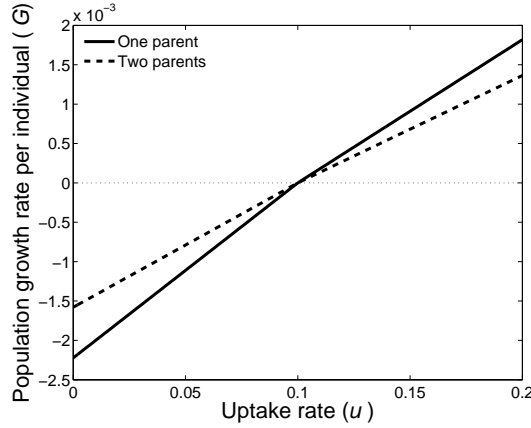

Fig. 2. Growth rates of individually and sexually reproducing populations. The parameters used were: $R_1 = 1.0$, $R_{\mathrm{r}}(1) = 0.1$, $R_{\mathrm{r}}(2) = 0.05$, $R_{\mathrm{c}} = 0.001$, and $R_{\mathrm{u}} = 0.01$.

The figure shows that the sexually reproducing population does in fact grow more slowly during population growth $(u > u_0)$. This is in line with the reasoning presented in Section 1 and Fig. 1. What is also evident from the figure is that the decline rate of the sexually reproducing population is lower in magnitude than that of the individually reproducing population. Furthermore, the two graphs diverge more as u gets further from u_0 indicating that fluctuations may be important, however the ratio between the two plots stays constant. Indeed, in this example, the growth rate of the sexually reproducing population is 0.75

that of the individually reproducing population. However, the decline rate of the sexually reproducing population is only 0.71 that of the individually reproducing population. Interestingly, the sexually reproducing population has a greater advantage during decline periods than the individual strategy has during growth periods.

This analysis therefore indicates that the ratio of growth and decline rates is important and that fluctuations might also be significant. Simple mathematical analysis can be done on the relative growth to decline rates for populations with different numbers of parents, this is given by:

$$\Psi(n) = \frac{G_{u > u_0}}{G_{u < u_0}} = \frac{R_1 - R_{\mathrm{r}}(n)}{R_1 + nR_{\mathrm{r}}(n)} \ . \tag{6}$$

It seems very likely that populations with larger values of Ψ will competitively exclude populations with lower values: this is tested with simulations in Section 2.2. In this model, the behaviour of Ψ depends on the way $R_{\mathrm{r}}(n)$ is determined.

I look at three scenarios for determining $R_{\mathrm{r}}(n)$. These consider the offspring cost which is defined as the total reproduction cost spent on each offspring (nR_{r}). In scenario (i), I consider the case where the total cost of each offspring is static: $R_{\mathrm{r}}(n) = R_{\mathrm{r}}(1)/n$. In this case, Equation (6) is increasing (the denominator is constant and the numerator increases). Scenario (ii) looks at the case where the cost of total cost of each offspring increases linearly with each extra parent: $R_{\mathrm{r}}(n) = R_{\mathrm{r}}(1)[1+c(n-1)]/n$ (c is a constant). Finally, in scenario (iii) I consider the case where Ψ is constant – i.e. when there is no advantage or disadvantage to reproducing with more parents. Simple manipulation of Equation (6) shows that if $\forall n : \Psi(n) = \Psi(1)$ then,

$$R_{\mathrm{r}}(n) = \frac{2R_{\mathrm{r}}(1)R_1}{R_1 + R_{\mathrm{r}}(1) + n[R_1 - R_{\mathrm{r}}(1)]} \ . \tag{7}$$

This sets an upper limit for the reproduction cost: if $R_{\mathrm{r}}(n)$ is above this value, then $\Psi(n) < \Psi(1)$, if $R_{\mathrm{r}}(n)$ is below this value then $\Psi(n) > \Psi(1)$.

The offspring cost is plotted in panel A of Fig. 3 for different numbers of parents in the three cases. Given the corresponding reproduction costs associated with these offspring costs, panel B shows the value of Ψ calculated by Equation (6).

As expected, the plot in Panel B of the figure shows how Ψ increases when the offspring cost is not dependent on the number of parents. The difference in values of Ψ is relatively high when the number of parents is low – the largest increase being the difference between individual and sexual reproduction. When the offspring cost increases linearly with the number of parents, Ψ reaches a maximum at 2 parents (sexual reproduction) and declines thereafter. Considering Panel A of the figure, this indicates that, as the number of parents increases, the total cost of reproduction spent (the cost per offspring) may increase. Again, this increases sharply as the number of parents increase from 1 to about 5 and then levels out. For all graphs, changes in parameters R_1 and R_{r} did not change the shape of the graphs significantly, however, as the ratio (R_1/R_{r}) decreases, the values generated by Equation (7) increase (not shown).
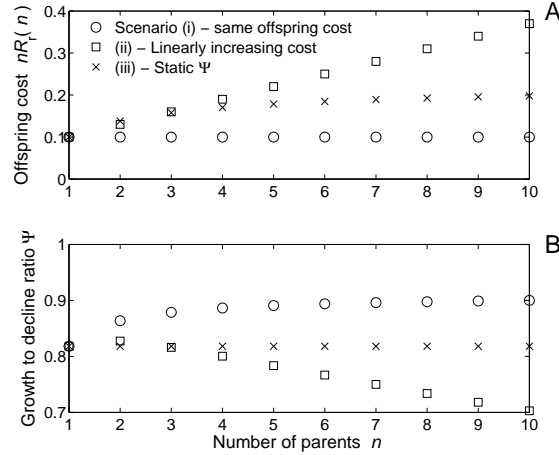
Fig. 3. The behaviour of the growth/decline ratio changes with different functions for $R_r(n)$. Panel A shows the cost per offspring generated by the three different functions of $R_r(n)$ and panel B shows the corresponding predicted growth to decline ratio. The parameters used were: $R_1 = 1.0$, $R_r(1) = 0.1$, $R_c = 0.001$, $R_u = 0.01$, and $c = 0.3$.

2.2 Simulation models

The predictions of the mathematical treatment in the previous section indicate two things that may be tested with simulation models. Firstly whether the value of Ψ is a good predictor for which strategy is optimal and secondly that fluctuations may also be significant.

Simulations are done with agents modelled as resource levels, based on Equation (1). At each timestep an agent pays a growth/maintenance cost R_c. When its resources are below zero, an agent will die. Each agent has a reproduction strategy which is defined by the number of parents (from 1 to 10) the agent will reproduce with. Those with the same reproduction strategy will reproduce when enough agents (depending on the number of parents defined by their common strategy) have resource levels that are above R_1 (resource levels may go above R_1 without penalty). Each parent pays a cost of reproduction $R_r(n)$ and all parents share their energy with the new offspring.

The simulation models are essentially non-spatial, with individuals located on a grid but moving to a random new cell each timestep.[1] Agents consume a resource unit if they encounter any on the square they are on. A number of resource units, each of value R_u are randomly scattered on a spatial grid (of 50×50 squares) each time step. The number of units is either static (set to 200) throughout the simulation, or fluctuated between two values (100 and 200) changing every 1,000 timesteps.

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[1] The results in [13] showed that agents receive resources with between-resource intervals on a geometric distribution when they move to random grid squares each time step

The simulations were run with the three scenarios for determining $R_r(n)$ presented in Section 2.1. All scenarios were tested with a static resource input to the system and fluctuating resources. The scenarios were run ten times, with each run initialised with a different random seed. After 1,000,000 timesteps the number of agents with each reproduction strategy was averaged over all ten runs. The results are plotted in Fig. 4.
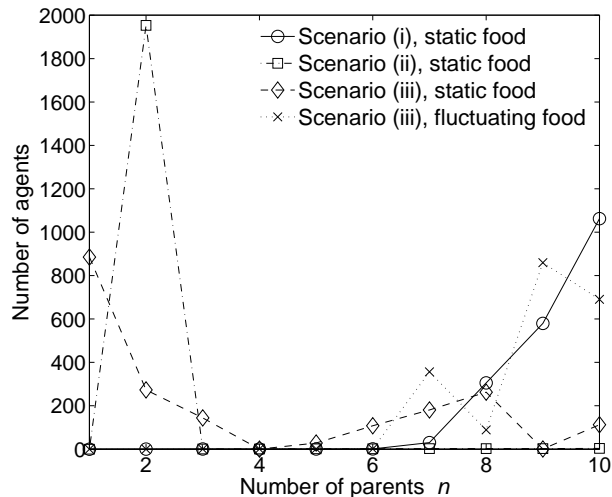

Fig. 4. Collective reproduction depends on offspring cost and resource fluctuations. Parameters for the simulations were: $R_1 = 1.0$, $R_r(1) = 0.1$, $R_c = 0.001$, and $R_u = 0.01$.

The figure shows that, when the offpring cost does not increase with the number of parents, reproduction strategies with higher numbers of parents will dominate. In fact any strategy with less than 7 parents has been completely eradicated from the simulations of this scenario. When fluctuations were also introduced, similar results were seen (not shown). When the cost per offspring increases linearly, the sexual strategy is dominant over the other strategies – as predicted by the shape of Ψ in Fig. 3. Again, the results were similar with and without fluctuations. When the cost per offspring increases in line with the upper limit predicted by Equation (7) (see Fig. 3, Panel A), the viability of collective reproduction depends on fluctuations in resource availablity. With no fluctuations, individual reproduction is dominant, but when the resources do fluctuate, collective reproduction is dominant.

3 Discussion

The mathematical model and simulations presented in this paper demonstrate collective reproduction. Individuals that may reproduce on their own, instead

reproduce as part of a collective. Collective reproduction here is done by sharing resources contributed to a shared offspring. The modelling work shows that the cost of this process (the cost of reproduction) is important and fluctuations in environmental resource levels can be significant. The model also presents two different scenarios which predict conditions for when sexual reproduction is optimal and other conditions for when reproduction in larger groups is optimal: this may help to explain why sexual reproduction is dominant in some animals and eusociality is dominant in others.

The mathematical predictions presented in Fig. 3 are concordant with the results in Fig. 4, both predicting when collective reproduction is viable. This includes subtle effects such as the dominance of sexually reproducing individuals. Since the results are so similar, the simulation models show that Ψ is good predictor for which reproduction strategies will competitively exclude others. The mathematical treatment is therefore instructive (in line with [14]) as to why there is a long term growth benefit to lineages that reproduce in this way: the collectively reproducing individuals have greater resources and are therefore less vulnerable to resource fluctuations.

The work contributes to explaining the rise in the complexity of the individual in two ways. Firstly, it demonstrates how collective reproduction can benefit both partners: when more than one parent contributes resources to the production of an offspring, the combined reproductive expenditure can be significantly larger than with individual parents (see Fig. 3 panel A, and corroborating simulation results in Fig. 4). This extra resource is available for the increased complexity needed for the facilitation of collective reproduction.

Indeed, it is plausible that collective reproduction may happen on many levels in the same class of individual. Some examples of collective reproduction may only be viable when the conditions are right, so different mechanisms for collective reproduction may happen under different conditions. Each may have different optimal numbers of parents. As well as this, collective reproduction may happen at different levels at the same time. With some organisms making direct genetic contributions, others making indirect genetic contributions (through kin-relatedness [7]) and others perhaps gambling their genetic contribution (see [15] for an example). There can therefore be many differing mechanisms of collective reproduction taking place within a population at the same time. As new viable mechanisms increase complexity, a rich social fabric should emerge.

Secondly, the model, and its insights, implies a potentially fruitful approach to modelling the major evolutionary transitions. Rather than invoking altruism or group selection, the model of collective reproduction presented here shows mutual benefits to reproducing collectively: i.e., that it is in an individual's selfish interest to reproduce collectively. There is no need for the individual to reduce its fitness for the benefit of its kin or its group. Altruism may therefore not be an essential feature in explaining the major transitions.

That said, this does not imply that altruism is not important in collective reproduction. Altruism can happen and will act as an evolutionary force when appropriate. One major assumption of the model is that the resources of all

parents are shared out equally between the parents and offspring. Clearly a parent that does not contribute in this way may be able to disrupt the process by contributing less resources than other parents. It could be argued that a parent that doesn't do this is acting altruistically, however by contributing less resources it will also be harming its own representation in the collective reproductive effort.

Study of such cheating behaviour is outside the scope of this paper but can be addressed in future work. Other future work could also address each of the major evolutionary transitions in more detail. It is to be hoped that the application of the style and approach of modelling in this paper will yield interesting results.

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