

Parental Investment and Reproductive Strategies

Steven Mascaro, Kevin B. Korb and Ann E. Nicholson

School of Computer Science and Software Engineering

Monash University, VIC 3800, Australia,

{stevenm, korb, ann}@csse.monash.edu.au

Abstract

Parental investment theory has been able to explain the evolution of investments by each sex in their children, across many species. It has also proved useful in predicting intra- and inter-sexual behaviour based on the investments made by each sex. We use an ALife simulation to investigate the effect of parental investment on various reproductive strategies – consensual mating, rape and abortion. Here, we describe the environment of this simulation in detail and also report empirical results from a range of experiments. These results include clear support for the view expressed by some evolutionary psychologists that differing parental investment after rape causes sexually dimorphic behaviour. We also touch on some preliminary results on the evolutionary stability of abortion.

Introduction

Organisms reproduce in many ways. A survey of reproductive methods raises the question of why organisms develop one form of reproduction over another. The notion that organisms are attempting to maximize their (inclusive or individual) fitness is a powerful organizing concept, but tends to require overly specific explanations of how fitness is being optimised. Theories of intermediate generality can be of help by simplifying explanations and thus highlighting what assists or diminishes fitness. In the case of reproduction, one such intermediate candidate is parental investment (PI) theory.

Parental investment is defined by Trivers as any investment by a parent in a child that increases the child's chance of survival and reproduction, at the cost of investing in other children (Trivers 1972). This definition allows us to see that, for a given species, members of the same sex typically invest in similar ways, while investments across the two sexes differ greatly. Trivers argues that these sex-based differences in parental investment are the ultimate causes of behavioural sexual dimorphism. Assuming this argument is correct, parental investment can be used to (1) explain the dimorphic behaviour of the sexes and (2) contribute to an explanation of the structure and behaviour of members from a single sex.

Most applications of parental investment theory have focused on dimorphism in consensual mating (or just *mating* in those organisms where the notion of consent does not apply). In contrast, we aim to apply parental investment theory to various reproductive strategies, namely consensual mating, rape and abortion. To this end, we employ an evolutionary ALife simulation to explore how parental investments corresponding to various actions affect these reproductive strategies.¹ In the case of consensual mating and rape, we examine how varying the difference in parental investment between the sexes affects sexual dimorphism; while in our early ALife experiments with abortion, we examine whether abortion, in regulating an agent's parental investment, is an evolutionarily stable strategy.

The use of an ALife simulation allows us to investigate questions about actions such as rape and abortion that would otherwise entail impractical and unethical experiments. Simulation experiments may be performed with no ethical concern about the experiments themselves, while taking care that the simulation model is an appropriate representation. Evolutionary analysis of human behaviour, particularly of rape and abortion, is a contentious area.² In this work we examine the agent actions of rape and abortion simply as actions whose frequencies have evolved in consequence of parental investments. Additionally, we consider rape solely as a sexual act to avoid complicating experimental considerations; this does not reflect our personal views of these actions in the human sphere. We do believe, however, that the ALife simulation presented in this paper can provide valuable insight into the possible evolution of these reproductive behaviours.

In the following section we review the relevant back-

¹The ALife environment is an extension of the one we have used in previous work investigating suicide as an evolutionarily stable strategy (Mascaro, Korb, & Nicholson 2001).

²On rape, the current view divides sharply between whether the motivation is primarily sexual (Thornhill & Palmer 2000) or whether it is a show of power, concerned with dominating and humiliating a victim (Sanday & Tobach 1985).

ground work on parental investment theory and evolutionary biological studies on reproductive behaviour. The ALife environment is then detailed briefly. In the main section of our paper we describe our ALife experiments and their results, first focusing on rape and then our initial experiments on abortion.

Background

Parental investment theory owes its beginnings to Bateman and his experiments on *Drosophila* (Bateman 1948). Bateman reasoned that the easy production of male gametes, and the slow and difficult production of female gametes (due to nutrition requirements), would cause intra-masculine competition (to seek opportunities for greater reproductive success) and greater discrimination of partners by females (to avoid wasting opportunities). He also suggested this would lead to greater variability in reproductive success for males than in females. Trivers later generalized Bateman's ideas with the notion of parental investment (Trivers 1972), expanding the focus from the physiological cost of reproduction to *any* form of contribution from parent to child.

Trivers defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." Importantly, this definition specifically excludes (1) any investments in mating attempts and (2) investments that might prevent other forms of reproductive effort of the parent. Removing these concerns from the scope of parental investment is important as it allows one to make predictions about them. Trivers subsequently speculated that the already large physiological investment made by the female in most species compels her to invest further, while the minimal investment made by the male in no way binds him to providing more. This latter idea was contested, however, by Dawkins & Carlisle (1976), observing that further investment must be assessed solely on the additional reproductive benefit the further investment itself confers.

There have been several other suggestions as to why one sex might invest more than another. One proposal is that where one parent suffices to raise a child, the sex that can desert first, will (Dawkins & Carlisle 1976). However, empirical results do not support the desertion hypothesis, since male parental care has been witnessed even in species where they have the first opportunity to desert (Krebs & Davies 1987). Another alternative explanation for differential investment is that of Williams (1975): if one parent finds itself in the vicinity of the child, due to another preadaptation, the basis for further parental care is established.

Studies of Rape and Abortion. While it is hard to find evolutionary biological literature that does not deal with (consensual) mating in some way, discussions of rape and abortion are a great deal more scarce. Recently, a handful of researchers have studied human rape on an evolutionary basis (Shields & Shields 1983; Thornhill & Thornhill 1983; Thornhill & Palmer 2000). They employ the concepts of female choice and male competition to explain the existence of rape, implicitly appealing to notions of parental investment. Their reports on rape tend to explicitly involve the prescriptive as well as the descriptive — in addition to their evolutionary explanation of rape, they also suggest what can be done to reduce rape rates; the assumption is that rape is primarily to do with reproduction.

Abortion has also been studied from an evolutionary perspective (Hrdy 1979; Hrdy & Hausfater 1984; Lycett & Dunbar 1999). Several researchers, particularly Hrdy, that have focused on various forms of abortion, infanticide and pedicide, intentionally drawing them all under the single term infanticide. With regard to abortion, they suggest that it exists in the animal world (to a degree greater than originally believed) because it sometimes allows the parent to increase its inclusive fitness over the alternative of allowing the pregnancy to carry to term.

Lycett & Dunbar (1999) have examined abortion rates specifically amongst humans and how they reflect parental investment considerations. Drawing on 1991 census data for England and Wales, they find that young single women and older married women are the most likely to perform abortions, which accords with their predictions based upon PI theory.

The ALife Environment

We now describe the simulation environments we have used in these studies. The simulation environment is not the same for every experiment in this study. In particular, the environment for the rape experiments differs from the environment for the abortion experiments and, although they do have much in common, these environments will require some separated discussion. We will describe features common to both environments first, proceed to their individual discussions when necessary, and then return to a discussion involving both environments on actions directly affecting reproduction.

The agents of the simulation live on a 40x40 board. Only one entity (either an agent or morsel of food) can inhabit a cell on this board at any given time. Agents have various numerical properties such as health, age and maximum age of death and nominal properties such as sex. Agents also have a genotype that specifies their behaviour probabilistically, from a set of simple actions, based on their environment. Each action an agent takes has an effect on that agent's health and utility, while

some actions also affect the health and utility of other agents.

Simulation Time. The simulation uses a *cycle* as a convenient unit of time; in each cycle all agents currently alive are given (in random order) a chance to perform some action. An agent’s age is measured in cycles since birth. Its maximum age is randomly selected (at birth) from the normal distribution $N(100, 10)$. A period of 5 cycles in the rape simulations (and of 50 cycles in the abortion simulations) is called an *epoch*; this unit of time is provided for statistics and used exclusively in the presentation of empirical results.

Agent Sex. Agents are either male or female, although since there are no gametes, the usual definitions of the two sexes cannot apply. Instead, we define the male sex to be the one that invests least in reproductions overall. Further, internal fertilization is assumed, so that females can never avoid a substantial parental investment.

Phenotype. There are from five to seven actions available to agents, depending upon the simulation configuration: eat, walk, turn, rest, consensual mate, rape and abortion. For brevity, consensual mating will be called ‘mate’. For the first four actions (those not related to reproduction), there is no difference between the sexes in the effect on health or the utilities. The choices of external entities for actions are blind. For instance, attempts at mate and rape will draw upon a random agent within the actor’s neighbourhood (ignoring sex), while the agent randomly selects food from its environment when eating.

Additionally, the generation of the probabilities in the genome of an agent at the start of the simulations is weighted in favour of eating and mating. These initially higher eating and mating probabilities allow stabler simulations, and the probabilities are free to evolve in any direction thereafter.

Parental Investments. The simulation model represents parental investment directly by numerical values that flow from the parent to the child. Importantly, parental investment is a property of the sex of an agent, not of the agent itself. The parental investments that agents provide do not evolve and are fixed for each sex throughout a simulation. The amount of parental investment varies depending on which reproductive action has been taken (mating or rape), the sex of the agent and, for females, whether the agent chooses to abort; the differing parental investments are based loosely on parental investment theory, as described in the paragraphs below. Briefly, during reproductive actions, the investment is transferred by lowering the parent’s health

by the amount of the investment, and adding that investment to the new-born’s health; during abortion, the amount that would subsequently have been invested due to an earlier mate is eliminated.

Now we provide separate treatments of the two simulation environments.

Environment 1: Environment for the Rape Experiments

Births and parental investment. Conception and birth are simultaneous events, and all parental investments that are to be transmitted from parent to child occur at that point.

Genotype. The genotype consists of a set of condition rules, each associated with a probability vector of actions (i.e., the genotype is a set of production rules). An agent’s genotype contains seven rules, where each rule contains exactly one condition for each of the following observables: self-health (i.e., the agent’s own health level), self-age, self-sex (one that triggers for each sex), local population density, local food density, and mate-request (whether a neighbouring agent has requested to mate). Each of the self-health, self-age, local population density and local food density conditions are met if the observable is greater than an evolvable value kept with that condition.

Production rule matching complicates matters since some conditions will trigger multiple rules, while other conditions will not trigger any rule. In our case, this last problem is overcome by the sex-linked rules, since at least one of these rules must trigger all the time. In the case where multiple rules trigger, there are several ways we could choose a single rule. It will be useful to first discuss a handful of these techniques that we ruled out, and then discuss the rule selection technique we settled upon for the rape experiments.

Firstly, we may treat the production rules as a list (rather than a set) and select the first rule that matches in this list. However, rules at the end of the list will tend to be triggered less often than rules at the start, and evolutionary selection will therefore concentrate on the first rules. Furthermore, rules further down in the list will continually, on reproduction, be placed under rules which differ from those in the parent. This means the conditions under which the rule triggers will vary greatly from parent to child — i.e. it’s as if the rules are inherited with enormous mutations. Such large mutation rates will obviously hinder evolution. Alternatively, we may also choose the rule that closest matches the conditions given. However, this technique suffers more acutely from the same problem as the previous technique since the decision as to whether the rule triggers is dependent upon *all* other matching rules, not just matches with rules above. The technique we adopted for the ex-

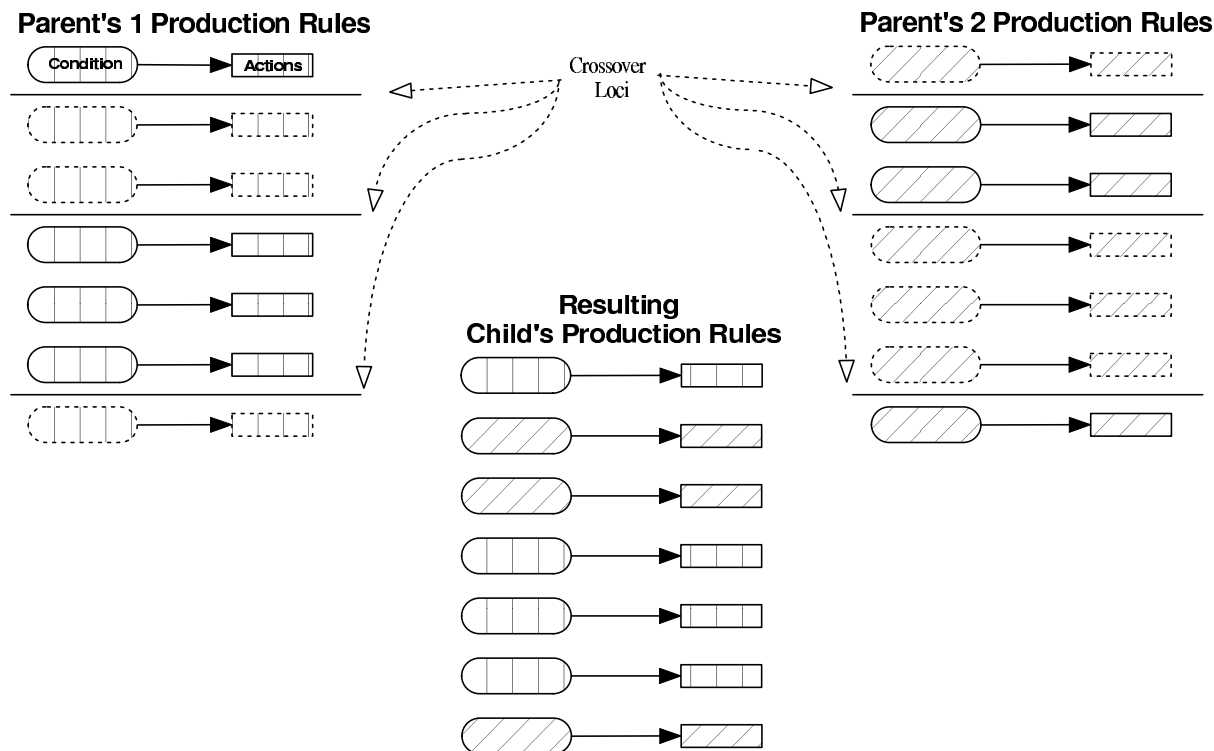


Figure 1: Example of a production rules crossover. Vertical shading indicates genes originally from **Parent 1**, diagonal shading indicates genes originally from **Parent 2**. In the parents, solid border lines indicate genes to be included in the child. Each row represents a rule, composed of a condition and a set of action probabilities (labeled 'Actions' in the diagram) to be used if the condition is met. There is one rule per observable condition (i.e. one for self-health, self-age, etc.) and so there are seven rules in an agent genome.

periments does not suffer from the above problems. Essentially, it involves randomly selecting a rule from the multiple rules triggered. This allows all rules to have an equal chance of execution, and also maintains the conditions under which a rule triggers when inherited by a child (on the average).

Reproduction. Recombination of the production rules is accomplished by a fixed-length, multi-point crossover on the rules in the genotype (see Figure 1); the number of crossover points can evolve through mutation. Values in the conditions and also the action probabilities undergo mutation according to mutation rates that are kept with each agent. These mutation rates themselves undergo mutation according to a *meta*-mutation rate kept with the simulation. This meta-mutation rate is constant for all the experiments.

From Genotype To Phenotype. The agent's genome animates the agent in the following way. When an agent's turn comes round in a cycle, a set of observations is made. Each rule in the agent's genome is examined in random order to see which ones match these observations (i.e. which ones trigger). The first rule that

triggers becomes the selected rule and this rule returns a set of action probabilities. The action to be performed for that cycle is then chosen stochastically and the action is carried out, assuming the agent can do so. The exception to this process is the triggering of the mate-request rule. An agent's mate-request rule is specifically triggered if and only if it receives a mate request. In this case, a consensual mating proceeds if the agent chooses to mate (from all available actions).

Environment 2: Environment for the Abortion Experiments

Births and parental investment. The experiments involving abortion require females go through a period of gestation. The length of the gestation period is a constant parameter for each simulation, but varies between simulations. The male gives all the health he is to invest in the child at conception. The female does not share any health with the child until birth. If she aborts during the gestation, she loses some of the health that she would have invested if the pregnancy was carried to term.

Genotype. The genotype used in the abortion experiments is basically a decision tree, where each branch

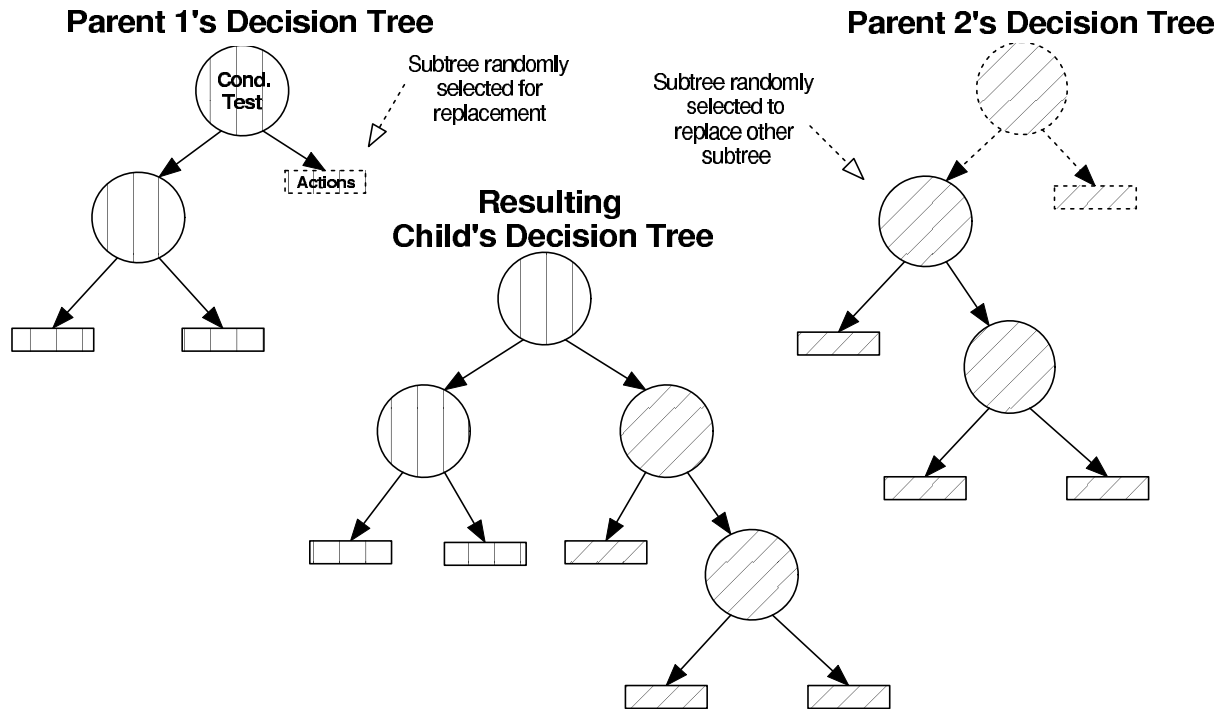


Figure 2: Example of a decision tree crossover. Vertical shading indicates genes originally from **Parent 1**, diagonal shading indicates genes originally from **Parent 2**. In the parents, solid border lines indicate genes to be included in the child.

node is for a specific observable (e.g., self-age) and possesses a single split value that partitions the observable values into two ranges. Each terminating leaf of the tree is a probability vector across actions, in the same way as for the rape experiments. Each path down the decision tree can be considered equivalent to a production rule. However, there are several differences to production rules genotypes that allow it to be more flexible. In this genotype, any number of conditions (for any observable) are allowed along a path of the decision tree (i.e. in a single rule). There can be any number of nodes and therefore paths (rules) and the observable for each node can be mutated to another observable. This genotype makes genetic analysis more complicated since most genomes will no longer be structurally identical, however it allows for greater evolutionary flexibility. In addition, this genotype does not suffer any of the problems of the genotype for rape experiments, since one rule and only one rule (a single path) will always be triggered. In this genome, along with the six kinds of conditions available to the rape experiments (i.e. those of self-health, self-age, etc.) agents have an additional condition called with-child, which indicates whether the agent is gestating.

Reproduction. Recombination of the decision trees is conceptually simple (see Figure 2). One parent's decision tree is selected as the basis for the child's decision

tree. A subtree (or in some cases the entire tree) is then taken at random from the other parent and replaces a randomly selected subtree in the child's decision tree. This subtree replacement only occurs once per reproduction (i.e. it is analogous to a single point crossover). Conditions and action probabilities are subject to mutation after recombination. For the conditions, the split values and the observables which the conditions use are both liable to mutation (in contrast to the production rules genotype, in which the observables are fixed). The mutation model is the same as for the rape experiment, in that each agent keeps their own mutation rates and these are subject to system-wide meta-mutation.

From Genotype To Phenotype. The agent's animation occurs in a similar way to the rape experiments with a few differences explained presently. When the agent makes its observations for the cycle, they are taken to the root node. Assuming the root node is a branch, the observed value corresponding to the root node's observable is tested against the root node's split value. When the observed value tests greater than the split value, all the observations travel the path to the right; correspondingly, when the observed value is lower than the split value, all the observations travel the path to the left. If another branch node is encountered on the newly travelled path, then the process recurs and there is another test between the value for this newly encoun-

tered node’s observable and the node’s split value. If, on the other hand, a leaf node is encountered, the recursion stops and the action probability vector for this leaf node is returned. The action to be performed for the cycle is chosen stochastically from this vector. In contrast to the rape experiments, paths with the mate-request observable are not triggered specifically when there is a mate request.

Actions Associated with Reproduction

Mating. Mating is the basic reproductive action. To mate, an agent signals its intentions to another candidate agent, and this other agent then indicates acceptance by also choosing to mate, or rejection of the request by choosing some other action. For the experiments without abortion, if the agents are of opposite sex and have sufficient health, they will produce a child. For the abortion experiments, the female will become pregnant, and go through a period of gestation, whose length is varied for the experiments between 2-8 cycles. In all experiments, unless otherwise noted, both male and female have the same parental investment after mating.

Rape. Rape is implemented as a distinct action that forces the victim to copulate when the initiating agent chooses. The victim suffers a heavy penalty through utility, while the perpetrator obtains a small positive utility. The parental investment by either the victim or the rapist is determined solely by the sex of the agent. It is assumed that the female will compensate for the lack of male investment, so that the sum of the parental investments made after rape will equal those made after mating. Hence, females may invest quite heavily, dependent upon the parental investment values set for mates. We allow for the possibility that an attempted rape is not completed (say due either to effective resistance by the victim, or outside assistance) through a simulation parameter called the rape-completion probability (rcp). If the perpetrator and the victim of rape are of opposite sex, and the victim has sufficient health for the set parental investment, the rape-completion probability is the chance a rape results in conception, in which case reproduction proceeds as per reproduction for mating.³

Abortion. In the abortion experiments, females have a gestation period during which they can abort. Abortion in the model causes pregnancy termination and saves health that would otherwise be used for parental investment in the child. Specifically, on conceiving an agent will invest half of its overall investment in the child.

³There is a comparable *mate-completion* probability (mcp) in the simulation, though it is not a directly specified parameter. It is equal to the probability that the target of a mate request is of opposite sex multiplied by the probability that the opposite sex target agrees to the mate.

If the agent aborts, no birth and no more investments occur and the agent is freed for other conceptions; if the agent does not abort, the child is born and the remaining half of the investment is transferred to the child. Abortion is available to *any* agent, be they gestating or otherwise, male or female, but it is simply ignored when a non-gestating agent chooses to abort.

Rape Experiments

In this section we investigate the factors affecting rape rates and sexual dimorphism through a range of simulation experiments. All results show the average of 30 simulation runs.

Varying Female Parental Investment after Rape

The first set of experiments varies the female parental investment after rape while keeping all other parameters in the simulation (including male investment) constant. The results are shown in Figure 3, for a varying rcp of (a) 0.1 (b) 0.25 and (c) 0.5. These graphs show the average rates for rape attempts for both females and males over the last 400 epochs of a 2000 epoch simulation run, as evolutionary equilibrium has been achieved by this stage. Note that the combined investments by both sexes during mating also increases in the same degree but with both sexes contributing equally. We can see that at $rcp=0.1$, regardless of how large female investment grows, there is little discernible difference between the rape rates.

More detail about the differences in male and female behaviour can be seen in Table 1. This table shows average female rates for eating, mating and rape actions over the last 400 epochs, together with the percentage increases needed to move from the female rape rate to the male rate (in parenthesis), for each female investment level. As the female investment increases (i.e., as the combined male and female investment increases), the rates of eating go down, while the mate and rape rates go up. This can be explained by agents being born with more health, and so needing to eat less in general. The most substantial difference between males and females in these three actions is for rape when female investment after rape is highest. It would appear that at $rcp=0.1$ a significant investment by females is necessary during rape before any dimorphic behaviour may become manifest.

As we increase the rcp ($rcp = 0.25$ in Figure 3(b)) differences between male and female rape rates become apparent as the female investment levels increase. These statistically significant differences are again apparent across all actions as shown in the middle section of Table 1. Note that as the female investment increases, the eating and mating rates also increase, though not as fast as the changes in rape behaviour. It is also interesting to note that, as female investment increases, female

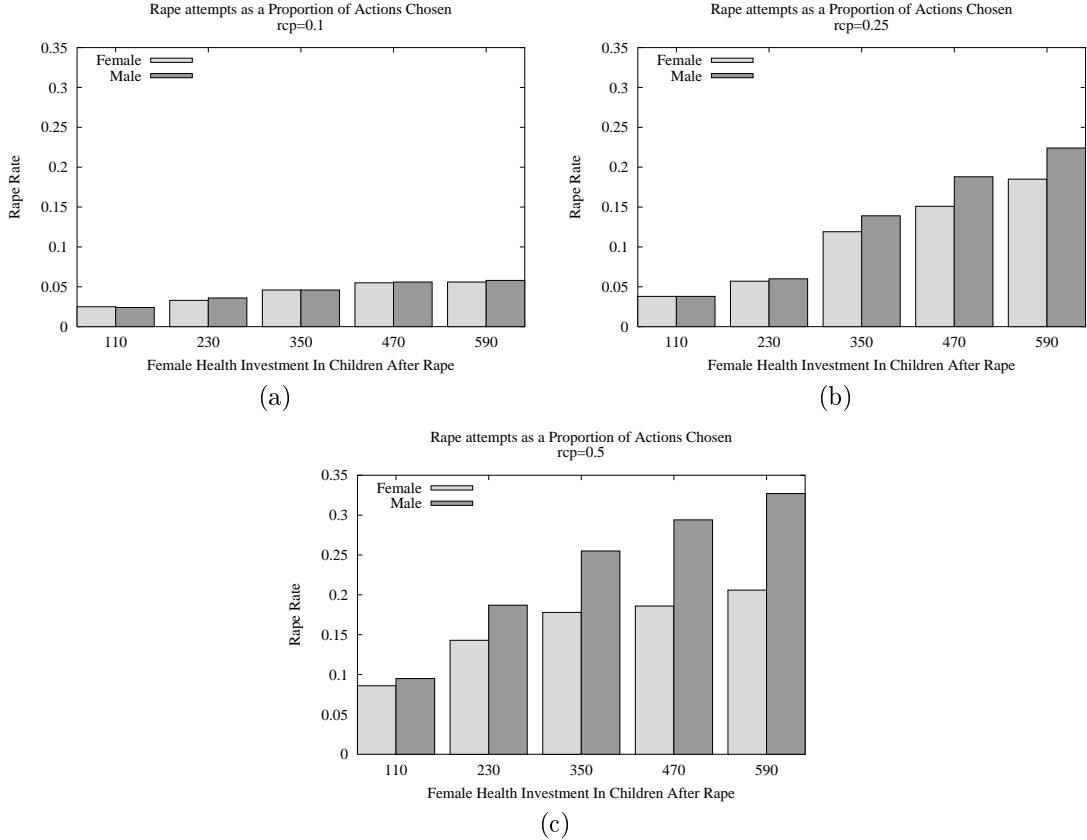


Figure 3: Female/Male rape rates for different levels of female parental investment and a fixed male parental investment (10 health units), for $rcp =$ (a) 0.1 (b) 0.25 and (c) 0.5.

rape rates increase, while female mate rates appear to remain fairly stable. At the lowest female investment, mate attempts outnumber rape attempts by 6 to 1, while for the highest female investment, the rates are roughly equivalent. Additionally, females have begun to eat significantly more than males to compensate for the heavy toll of their investments. Interestingly, average female health is marginally higher than average male health for the $rcp = 0.25$ simulations (997 to 975 units when female investment is 590 units), but with greater variance (female S.D. is 580, male S.D. is 527). For the $rcp = 0.5$ simulations, average female health becomes less than the average health for males (664 to 781 units), and now with smaller variance (female S.D. is 417, male S.D. is 430).

The results for the $rcp=0.5$ (see Figure 3(c) and bottom section, Table 1) show very strongly sexually dimorphic behaviour results, even with the lowest setting for female investment. Rape also becomes the predominant reproductive method, so the cost of rape appears to have been offset by the increased chance (due to the higher rcp) of producing a child.

So, while lower probabilities of rape completion produce a more realistic number of rapes, differences are most apparent with higher probabilities. As female in-

vestments grow, so do the differences in rape rates, with males performing the bulk of the rapes. Additionally, mate attempts by males also increases over attempts by females, and females compensate for their lower health by eating more.

We would also like to see if the dimorphism in rape behaviour has caused greater variability in the reproductive success of males than of females. Figure 4 shows the frequencies of numbers of children per agent when $rcp=0.25$ and 0.5. The frequency polygon of the male is flatter than the female's in both graphs (this difference is greatest when $rcp=0.5$), hence the male's reproductive success is indeed more variable.⁴

Additional Rape Experiments

We also ran several other experiments whose results we shall discuss only briefly. In one of these experiments we relaxed the assumption of symmetrical investments after mating. We found that, as expected, sexual dimorphism in mating increases slightly with greater female investment (see Figure 5(a)), while the differences in rape rates

⁴For the final version of the paper, we intend to add graphs of variability in offspring number for mate-only (no rape) simulations containing dimorphic investments after mate.

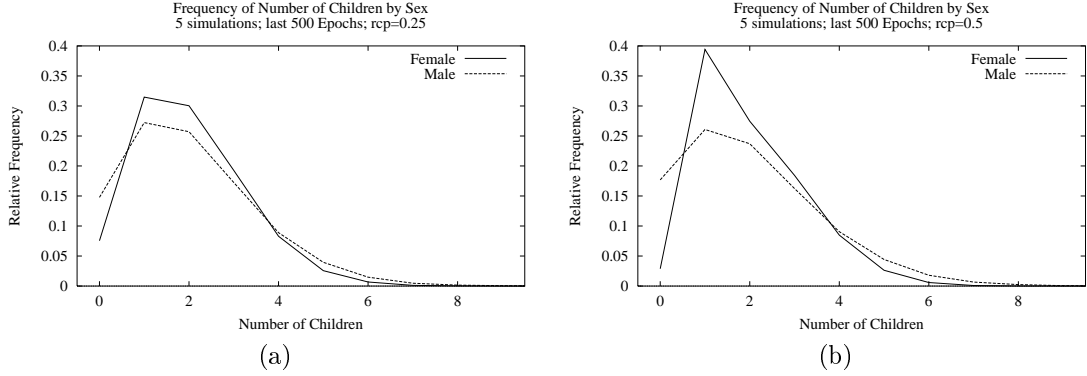


Figure 4: Frequencies of the number of children per agent in simulations with rcp equal to (a) 0.25 and (b) 0.5.

Female Investment	Eat	Mate	Rape
$rcp=0.1$			
110	0.547 (-1.0%)	0.266 (1.8%)	0.025 (-1.1%)
230	0.487 (-0.7%)	<i>0.311 (-0.3%)</i>	0.033 (1.8%)
350	0.422 (-1.9%)	0.362 (0.7%)	<i>0.046 (-0.6%)</i>
470	<i>0.377 (-0.2%)</i>	<i>0.384 (-0.2%)</i>	0.055 (1.0%)
590	0.361 (0.5%)	0.392 (0.7%)	0.056 (3.2%)
$rcp=0.25$			
110	0.562 (-2.2%)	<i>0.245 (0.7%)</i>	<i>0.038 (-0.3%)</i>
230	0.518 (-1.8%)	0.252 (4.7%)	0.057 (5.9%)
350	0.436 (-7.7%)	0.266 (1.1%)	0.119 (17.1%)
470	0.421 (-12.6%)	0.239 (8.6%)	0.151 (24.2%)
590	0.415 (-19.7%)	0.210 (15.0%)	0.185 (21.0%)
$rcp=0.5$			
110	0.590 (-2.9%)	<i>0.180 (0.6%)</i>	0.086 (9.9%)
230	0.597 (-10.3%)	0.108 (7.5%)	0.143 (30.9%)
350	0.596 (-18.3%)	0.071 (19.1%)	0.178 (43.4%)
470	0.568 (-21.3%)	0.085 (4.8%)	0.186 (57.9%)
590	0.549 (-28.2%)	0.074 (35.4%)	0.206 (58.8%)

Table 1: A table of the eating, mate and rape attempt rates for simulations with different (fixed) female investment and rcp (0.1, 0.25 and 0.5). Numbers outside of parentheses show the relative frequencies with which **females** have attempted that action. Numbers inside parentheses show the difference between the male and female frequencies as a percentage of the female frequencies. Italicised entries did not show statistically significant differences between males and females ($p < 0.001$).

are affected very little by the variation in mating investments (Figure 5(b)); additionally, there was an increase in eating by females.

In another set of experiments, we tried to find circumstances that reduced sexual dimorphism. We have already seen that sexual dimorphism does not result when the rcp is low, and the female investment is not sufficiently greater than the male investment. We posited that the dimorphism would also be reduced if we were to somehow compensate females for the heavy cost of rape. We found that the dimorphism is, in fact, diminished (but not eliminated) when (1) females obtain a very high utility from initiating rapes and (2) males derive substantially less health from food.

Genetic Causes of Rape and Dimorphic Behaviour

Now that we have generated sexually dimorphic behaviour in our simulation, it is appropriate to investigate the genetic causes by looking at the conditioning of agent actions within the genotype. We would expect that the only rules that could induce sexually dimorphic rape behaviour are those that examine self-sex (obviously) and self-health, due to different parental investments causing different average healths for each sex. Mate-request observations may be involved in a difference in mate behaviour if one sex requests mates more often than the other, but will not cause a difference in rape. There is no reason to believe that other observation conditioning (on ages, food densities or population densities) will differ between the sexes to the extent of causing significant dimorphic behaviour; we certainly found no difference in our simulations.

We can see how much of the sex difference in rape rates is due to the difference in rape probabilities in the sex-specific rules. The average difference (across all agents) in the probability of rape between the female and male rules will indicate the contribution these rules make to the observed differences in rape rates. Figure 6(a) shows the increasing difference in the male and female rape probabilities (in the runs with $rcp=0.25$ and female investment at 590 health units), suggesting that the sex-linked rules are indeed contributing substantially to the difference in rape rates.

Now we isolate the effect of the self-health rules, in order to check their contribution to the difference in rape rates. We do this by taking the average rape probabilities from the health rules across all agents with a high value condition, and subtracting the average rape probability of the non-sex-linked rules.⁵ Figure 6(b) shows this statistic for the same runs as before. We can see a much larger difference here than in Figure 6(a), which

⁵We omit both sex-linked rules as the male rule may cause bias.

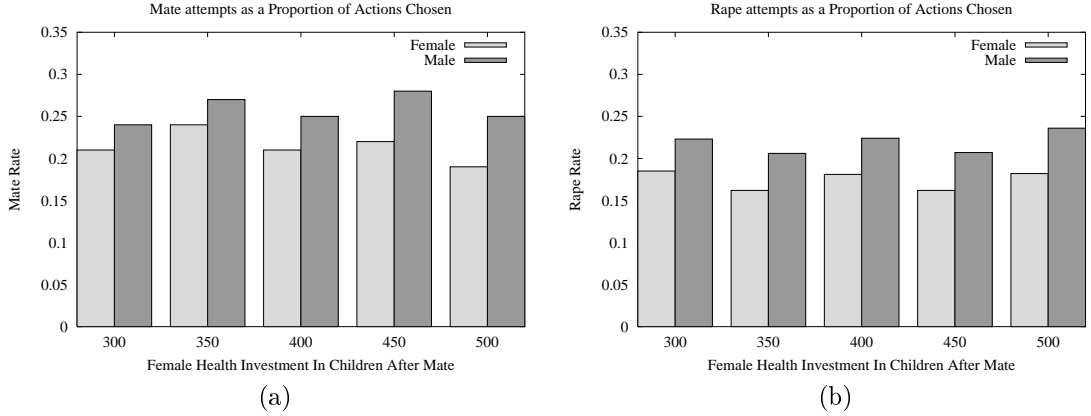


Figure 5: Female/Male (a) mate and (b) rape rates for different female and male parental investments after mating ($rcp = 0.25$). The male investments are equal to 600 minus the female investment.

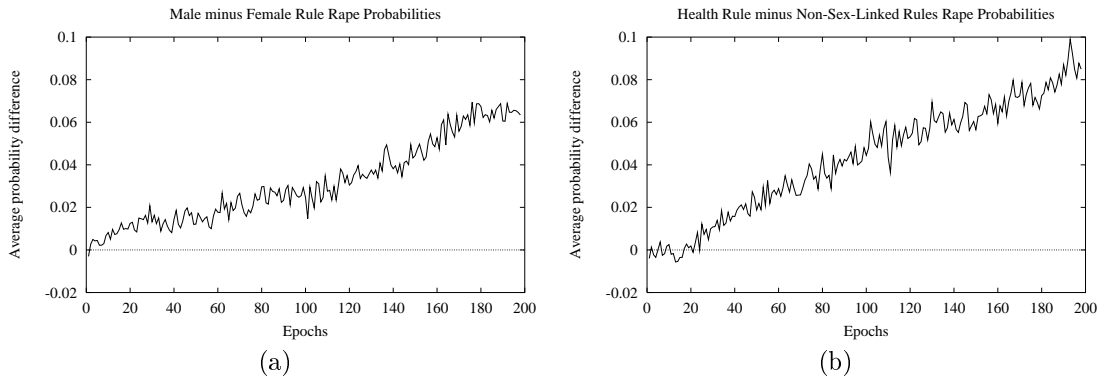


Figure 6: (a) The average male minus female probability of rape in the genome for the $rcp=0.25$ runs from Figure 3(b). (b) The average probability of rape in high health rules minus the average probability of all other non-sex-linked rules.

would indicate that high health makes a slightly greater contribution to the difference in rape rates than sex observations.

Another interesting question is whether any sexually dimorphic behaviour results when agents are restricted to conditioning on sex alone. The graphs in Figure 7 are the result of runs where all but the female and male rules in the agent’s genotype have been eliminated; effectively, the genotype consists solely of female and male action probability vectors. There are still differences between male and female rape rates, however it is reduced for $rcp = 0.25$ runs (Figure 7(a)) and increased for $rcp=0.5$ runs (Figure 7(b)). Obviously, at the lower rape completion probability, it is harder for a benefit from dimorphic behaviour to appear when health is not taken into account — whereas, at the higher probability the benefits would be much more readily realizable.

Summary of Rape Results

We have shown that differential parental investments by the sexes in rape can produce sexually dimorphic rape behaviour. In particular, we have shown that as the

difference in investments increase, the lesser investing sex comes to attempt rape more than the greater investing sex. This effect is moderated by the probability that the rape will result in conception. Additionally, we have shown that differential investments after mating do not necessarily cause a change in rape behaviour.

Initial Abortion Experiments

Our abortion experiments, in contrast to the previous ones on rape, will have nothing relevant to say about sexual dimorphism; instead, we are interested in seeing whether abortion can be evolutionarily stable, and how its effects on parental investment affect an agent’s overall reproductive strategies. At this initial stage, we have only investigated whether abortion can be an evolutionarily stable strategy (ESS), and are currently pursuing further work related to abortion.

We use the term ESS in the manner defined by John Maynard Smith as “a strategy such that, if all the members of a population adopt it, then no mutant strategy could invade the population under the influence of nat-

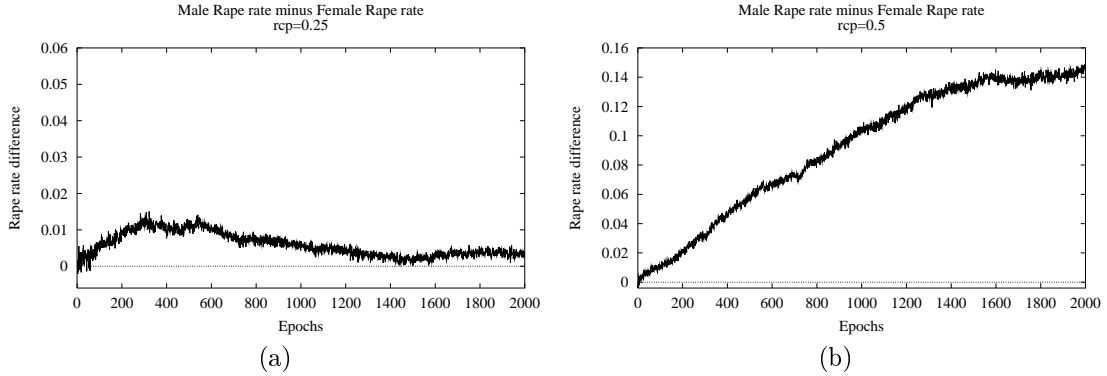


Figure 7: The rape rate difference between sexes for (a) 0.25 probability of rape completion and (b) 0.5 probability of rape completion when sex is the only observation allowed.

ural selection” (Maynard Smith 1982). In our experiments, strategies are always mixed (i.e., probabilistic); therefore, the criterion for an ESS we apply is to test whether the behaviour resists disappearing in the presence of alternative behaviours.

There is a small problem in applying this notion of an ESS to our experiments: the simulation does not allow actions to disappear. An action whose genetic probability has fallen through evolution to 0 can always become active again through mutation. Mutation acts constantly, hence an action will never disappear.⁶ To work around this, we see if the action’s probability has dropped as low as it can be expected given this mutation (i.e. if it has fallen to the background mutation rate). If the probability could drop further, the action is an ESS, otherwise, it is not.

We can guess when abortion might be an ESS by considering when its effect on parental investment benefits the agent’s fitness. By an abortion a pregnant agent avoids a birth, and so the agent saves the parental investment required for a birth. However, these effects also come about if the agent avoids the mating that caused the pregnancy in the first place. In fact, abstinence will save the agent more health than mating followed by aborting, so abortion seems redundant. However, the crucial distinction between abortion and abstinence is elapsed time. An agent can: mate; mate and abort later; or abstain (perform some other action). If an agent cannot anticipate its future, the better strategy might be to mate now, and abort later if conditions have become worse. The environment in our simulations

⁶This is mitigated somewhat by the genetic representation for probabilities being allowed to move outside the range $[0, 1]$, but there is still the possibility of re-introduction through mutation. Specifically, in converting a vector of these ‘pseudo-probabilities’ to a vector of real probabilities, positive values are normalized to the range $[0, 1]$, while negative values are *clipped to 0*. Therefore, selection pressures to move the pseudo-probability *below 0* will not exist. Instead, mutation will produce a random-walk.

allows agents to interact randomly, and that food will be more or less plentiful in different sections of the board; hence situations in which agents conditions have changed after falling pregnant are likely to arise, and therefore we expect abortion will be an ESS in our simulations.

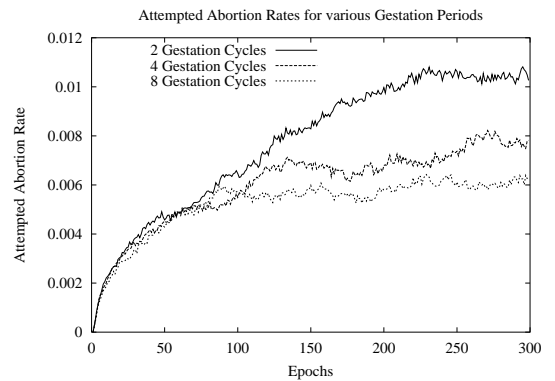


Figure 8: Abortion attempt rates at different lengths of gestation period.

Figure 8 shows the rates of abortion attempts for simulations where agents have different gestation periods. The simulations with a gestation period of two cycles must be showing abortion to be an ESS, since their abortion rates are significantly higher than those in the other simulations — i.e., the rate has not dropped as low as it could go. There is, however, a more direct way we can test if abortion is an ESS. We can check for a statistically significant difference between the average genetic abortion attempt probability and the distribution with mean 0 and variance equal to the mutation variance.⁷ We performed this test for each of the gestation periods over the last 150 epochs of the 300 epoch simulation

⁷Note that the tests applied to attempted abortions, since those are the operators available to our agents; some of the abortion attempts will have failed due to environmental conditions.

runs (recalling that epochs here are equal to 50 cycles) and obtained statistical significance for all simulations ($p < 0.001$; for each test, z fell in the range (4.52, 5.44)).

Conclusion

We have demonstrated the potential of ALife simulation to provide a vehicle for testing some of the theories of evolutionary psychology. Our experiments, while preliminary, offer support for some of the ideas of evolutionary psychology and, in particular, the story which parental investment theory tells of sexually dimorphic behaviour. We have also begun examining experimentally the evolutionary advantages and disadvantages of having the option to abort. Since the experimental or observational study of such matters in ethology and anthropology are difficult and contentious, we believe that our techniques offer an important supplement to such field research.

References

- Bateman, A. J. 1948. Intra-sexual selection in drosophila. *Heredity* 2:349–368.
- Dawkins, R., and Carlisle, T. R. 1976. Parental investment, mate desertion and a fallacy. *Nature* 262:131–133.
- Hrdy, S. B., and Hausfater, G. 1984. Comparative and evolutionary perspectives on infanticide: Introduction and overview.
- Hrdy, S. B. 1979. Infanticide among animals: A review, classification and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology* 1:13–40.
- Krebs, J., and Davies, N. 1987. *An Introduction to Behavioral Ecology*. Boston: Blackwell Scientific Publications.
- Lycett, J. E., and Dunbar, R. 1999. Abortion rates reflect optimisation of parental investment strategies. *Proceedings of the Royal Society, B: Biological Sciences* 266(1436):2355–2358.
- Mascaro, S.; Korb, K. B.; and Nicholson, A. E. 2001. Suicide as an evolutionarily stable strategy. In *Proceedings of the 6th European Conference on Advances in Artificial Life - ECAL 2001*, 120–132. Springer-Verlag.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge University Press.
- Sanday, S. R., and Tobach, E., eds. 1985. *Violence Against Women: A Critique of the Sociobiology of Rape*. New York: Gordian Press.
- Shields, W., and Shields, L. 1983. Forcible rape: an evolutionary perspective. *Ethology and Sociobiology* 4:115–136.
- Thornhill, R., and Palmer, C. T. 2000. *A Natural History of Rape*. London: Cambridge, Mass.
- Thornhill, R., and Thornhill, N. W. 1983. Human rape: An evolutionary analysis. *Ethology and Sociobiology* 4(3):137–173.
- Trivers, R. L. 1972. Parental investment and sexual selection. In Campbell, B., ed., *Sexual Selection and the Descent of Man*. London: Heinemann. 136–179.
- Williams, G. 1975. *Sex and Evolution*. Princeton, New Jersey: Princeton University Press.