

ALife Investigation of Parental Investment in Reproductive Strategies

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Abstract

Many organisms nourish and care for their offspring, boosting the offspring’s reproductive potential. Trivers (1972) recognized that such parental investment, when made differentially across the sexes, could explain the existence of sexually dimorphic behaviour. However, parental investment in nature is difficult to measure, and explanations involving parental investment are hard to verify. Here we use an ALife simulation to investigate the effect of explicit, numerical parental investments on two reproductive strategies of interest — consensual mating and rape. With some preliminary empirical results, we demonstrate the potential of an ALife approach to evolutionary psychology.

Introduction

Organisms reproduce in many ways, raising the question of why organisms develop one form of reproduction over another. Parental investment theory can help answer such a question. Parental investment (PI) is defined by Trivers as any investment by a parent in an offspring that increases the offspring’s chance of survival and reproduction, at the cost of investing in other offspring (Trivers 1972). For many 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 PI are the ultimate causes of behavioural sexual dimorphism.

PI is hard to measure in the real world, complicating efforts to test PI theory. Also, most applications of the theory have focused on dimorphism in consensual mating (or just *mating* when the notion of consent does not apply). We apply PI theory to the reproductive strategies of consensual mating and rape and in the process demonstrate a new ALife method of investigation for studies in evolutionary psychology. To this end, we employ our simulation to explore how numerically-expressed PIs corresponding to various actions affect reproductive strategies.¹ We examine how varying the PI across the sexes

produces sexual dimorphism with particular regard to consensual mating and rape.

Evolutionary psychology, particularly in the study of rape, is a contentious field. Along with most evolutionary psychologists, we take the view that behaviour is a product of many historical factors, with evolution being one. We suggest that the use of ALife simulations in evolutionary psychology give us the means to experiment with these factors. Such simulations could provide important insights not possible through traditional research or mathematical techniques. Our efforts here are primarily aimed at demonstrating the potential of ALife simulations in evolutionary psychology.

In the following section we review the relevant background on PI theory and evolutionary biology. We then detail briefly the ALife environment, before describing our ALife experiments and their results.

Background

PI theory began with Bateman (1948) and his experiments on *Drosophila*, but was formally described by Trivers (1972). Parental investment is “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.”

Fundamental to PI theory has been the sexually distinct PIs evident in nature. There have been several suggestions as to why the sex-based differences in PIs might occur. Trivers speculated that the already large physiological PI made by the female in most species compels her to invest further, while the minimal PI made by the male in no way binds him to providing more. This idea was contested, however, by Dawkins & Carlisle (1976), who asserted that further PI must be assessed solely on the additional reproductive benefit that extra investment confers. Instead, they proposed another hypothesis: where one parent suffices to raise an offspring, the sex that can desert first, will. For instance, amongst teleost fish where females have the first opportunity to desert, paternal care is common, even though the female provides the initially larger investment. However,

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).

empirical results with other species do not support the desertion hypothesis (Krebs & Davies 1987). A popular alternative explanation for differential PI is that of Williams (1975): if one parent finds itself in the vicinity of the offspring, due to another preadaptation, the basis for further parental care is established.

Maynard Smith (1977) analyzes parental investment theory from a game-theoretic perspective, giving equations for conditions that would lead to desertion by either one or both parents. This gives mathematical form to the scope and consequences of parental investment theory.

Recently, a handful of researchers have studied human rape on an evolutionary basis (Shields & Shields 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 PI. A problem common to all investigations of PI in nature, including these, is the difficulty of assessing the amount of investment made. How can one quantify the cost to parents of feeding and protecting their offspring and the benefit offspring derive? Game-theoretic models can provide greater detail to our analyses, however they deal with a form of PI very distant from that in nature. Simulation, however, can provide an alternative for testing our hypotheses in which parental investments are clear.²

The ALife Environment

The agents of our ALife simulation live on a 40×40 board. Only one entity (an agent or food) can inhabit a cell on this board at any given time. A certain amount of food is generated per cycle for the agents to eat. 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 (physical well-being) and utility (psychological reward — which feeds into health), while some actions also affect the health and utility of other agents. The specific effects of each action on health and utility are detailed further on.

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 $N(100, 100)$. A period of 5 cycles in the simulations is called an *epoch*; this unit of time is provided for statistics and used exclusively in the presentation of empirical results.

²The epistemological problems posed by ALife simulation are important, impacting far more than our study. We will be exploring them in future.

	Female H.E.	Util	Male H.E.	Util
Mate				
With Birth	$-PI$	15	$-PI$	15
No Birth	-16	15	-16	15
Unsuccessful	-5	-5	-5	-5
Request Denied	0	0	0	0
Rape (Victim)				
With Birth	$-(2PI - 10)$	-70	-10	-70
No Birth	-10	-70	-10	-70
Unsuccessful	-10	-10	-10	-10
Rape (Rapist)				
With Birth	$-(2PI - 10)$	5	-10	5
No Birth	-10	5	-10	5
Unsuccessful	-60	-15	-60	-15

Table 1: The health effects and utilities associated with reproductive actions. PI stands for the value of the parental investment parameter for the current simulation.

Agents are either male or female, sex being randomly determined at birth. Since there are no gametes, we define the male sex to be the one that invests least after mating, which is consistent with most species in nature.

Genotype. The decision of which action to perform in a cycle is determined by the agent’s chromosome. Viewed functionally, the chromosome accepts a set of observations for the agent and returns its action. Structurally, the genotype is a set of production rules or condition-action pairs: each observable has a corresponding conditional. A condition has a fixed comparator (e.g., *greater than*) and an evolvable value in $[0,1]$. An example might be ‘ $x > 0.4$ ’, where x is self-age (the agent’s age) divided by the maximum age. There are seven production rules in each chromosome: two for self-sex (one rule that matches females and another that matches males) and five conditioning upon self-health, self-age, self-sex, local population density, local food density and whether a mating has been requested. At each cycle every rule’s condition is checked for a match, in random order. Given a match, the rule’s probability distribution is used to choose an action.

Recombination of the production rules is straightforward, using multi-point crossover of the two parent chromosomes at gene boundaries. Condition values and action probabilities are subject to Gaussian mutation after recombination.

Phenotype. There are six basic actions available to agents: eat, walk, turn, rest, consensual mate and rape. For brevity, consensual mating will be called ‘mate’. A table of the health effects and utilities for reproductive actions can be seen in Table 1. These are not the only possible values that could be used, however we do suggest that they are plausible across a broad range of envi-

ronments of interest. For all actions except rape, there is no difference between the sexes in the effect on health or utility. Agents choose neighboring entities for actions randomly. To ensure initial stability, generated genetic probabilities for eating and mating are initially high, but can freely evolve thereafter.

Parental Investments. The simulation model represents PI directly by health flows from parent to offspring. In these simulations, the PIs are fixed for each sex.

Mating. Mating is the basic reproductive action. To mate, an agent requests mating another agent, who can then accept or reject. If the agents are of opposite sex and have sufficient health, they produce an offspring. In these experiments, unless otherwise noted, both male and female provide the same PI after mating.

Rape. Rape forces the victim to copulate when an initiating agent chooses. The victim suffers a heavy utility penalty, while the perpetrator obtains a small positive utility. Victims and perpetrators can be either male or female. We allow attempted rapes to fail through the parameter, rape-completion probability (rcp). If the rapist and victim are of opposite sex, and the victim has sufficient health, the rape-completion probability is the chance that a rape results in conception.

Experiments

We investigated two factors affecting rape rates and sexual dimorphism: female PI and the rcp . All results show the average of 30 simulation runs, unless otherwise stated.³

Figure 1 shows the effect of these two parameters on the rape rate. Each graph represents an rcp of (a) 0.1 (b) 0.25 and (c) 0.5, while within each graph, along the x -axis, are the various female PI levels (the fixed male PI is 10 health units).⁴ The combined PIs by both sexes after mating also increases to the same degree but with both sexes contributing equally. The graphs show the average rates for rape attempts for females and males over the last 400 epochs of a 2000 epoch run, after equilibrium has been achieved. We can see that at $rcp=0.1$, regardless of how large we set female PI, there is little discernible difference between the rape rates.

More detail about the differences in male and female behaviour can be seen in Table 2. This table shows average female rates for eating, mating and rape actions, together with the percentage changes to reach the male rate (in parenthesis), for each female PI level. As the female PI increases (i.e., as the combined male and female PI increases), the rates of eating go down, while the mate and rape rates go up. This can be explained

³A fuller description of our experiments can be found in (Mascaro, Korb, & Nicholson 2002).

⁴The PIs are in units of health. For context, the distribution of female health has roughly a mean of 800 and a s.d. of 500, while males have a similar s.d., but a mean health 100 units higher.

female PI	Eat	Mate	Rape
<i>rcp=0.1</i>			
110	0.547 (-1.0%)	0.266 (1.8%)	0.025 (-1.1%)
230	0.487 (-0.7%)	<i>0.311</i> (-0.3%)	0.033 (1.8%)
350	0.422 (-1.9%)	0.362 (0.7%)	<i>0.046</i> (-0.6%)
470	<i>0.377</i> (-0.2%)	<i>0.384</i> (-0.2%)	0.055 (1.0%)
590	0.361 (0.5%)	0.392 (0.7%)	0.056 (3.2%)
<i>rcp=0.25</i>			
110	0.562 (-2.2%)	<i>0.245</i> (0.7%)	<i>0.038</i> (-0.3%)
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%)
<i>rcp=0.5</i>			
110	0.590 (-2.9%)	<i>0.180</i> (0.6%)	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 2: A table of the eating, mate and rape attempt rates for simulations with different (fixed) female PI and rcp (0.1, 0.25 and 0.5). Numbers show the frequencies with which **females** have attempted that action. Parenthetical numbers show the difference between male and female frequencies as a percentage of female frequencies. Italicized entries did not show statistically significant differences between males and females ($p < 0.001$).

by agents being born with more health, and so needing to eat less in general.

As we increase the rcp ($rcp = 0.25$ in Figure 1(b)) differences between male and female rape rates become apparent as the female PI levels increase. These statistically significant differences are again apparent across all actions as shown in the middle section of Table 2. The results for the $rcp=0.5$ (see Figure 1(c) and bottom section, Table 2) extend this trend. We can see that very strongly sexually dimorphic behaviour results, even with the lowest setting for female PI. Rape also becomes the predominant reproductive method for both females and males, so the cost of rape appears to have been offset by the increased chance (due to the higher rcp) of producing an offspring.

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 (something that is very difficult to assess in nature). Figure 2 shows the frequencies of numbers of offspring 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.

We subsequently examined the agents' chromosomes to see which rules were causing the differences in rape behaviour. We found that the rules examining self-sex and self-health were the rules producing the sexually dimorphic behaviour. In particular, rules that triggered when the agent was male produced higher rape probabilities than when the agent was female. Furthermore, high

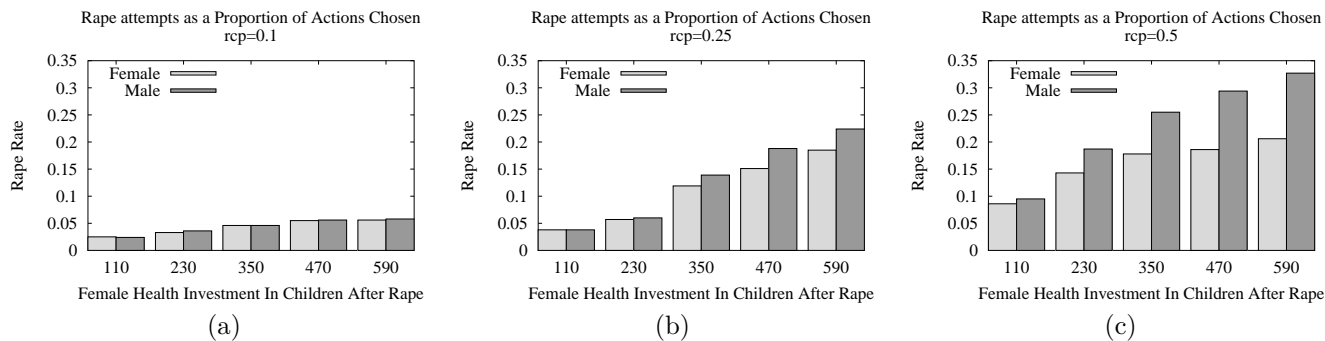


Figure 1: Rape rates for different levels of female PI (male PI = 10), for $rcp =$ (a) 0.1 (b) 0.25 and (c) 0.5.

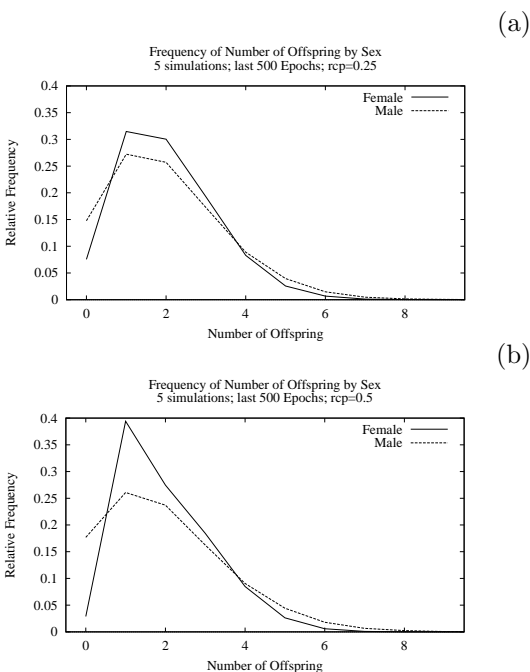


Figure 2: Frequency of number of offspring per agent with rcp equal to (a) 0.25 and (b) 0.5.

health triggered rules with higher rape probabilities than low health. In all runs, males had higher average health than females, so this would have further contributed to the sexual dimorphism. We also ran several other simulation variations in order to test the robustness of our results. In one of these experiments we relaxed the assumption of symmetrical investments after mating. We found that, as expected, sexual differences in mating increase slightly with greater female investment, while the differences in rape rates are affected very little.

Conclusions and Further Work

We have demonstrated that ALife simulations can test the theories of evolutionary psychology. Our experiments, while preliminary, even offer support for some

aspects of evolutionary psychology and, in particular, the story which PI theory tells of sexually dimorphic behaviour. We are currently extending our reproductive strategy experiments to abortion in order to see what conditions lead to the fatal termination of PI. In general, we intend to provide a fuller investigation of some of the issues central to PI theory, including an investigation of the evolution of differential parental investments.

Since the experimental or observational study of these matters in ethology and anthropology are difficult, we believe that our techniques offer an important supplement to such field research.

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