

## Chapter 1

# An ALife investigation on the origins of dimorphic parental investments

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When Trivers [13] introduced the concept of parental investment to evolutionary theory, he clarified many of the issues surrounding sexual selection. In particular, he demonstrated how sex differences in parental investment can explain how sexually dimorphic structure and behaviour develops in a species. However, the origins of dimorphic parental investments also need explanation. Trivers and others have suggested several hypotheses, including ones based on prior investment, desertion, paternal uncertainty, association with the offspring and chance dimorphism. In this paper, we explore these hypotheses within the setting of an ALife simulation. We find support for all these alternatives, barring the prior investment hypothesis.

### 1.1 Introduction

The issue of sexual selection has been hotly debated ever since Darwin raised its possibility. Darwin noted that the females of most species tend to be choosier and less competitive than the males. Bateman later gave this observation further support with his experiments with *Drosophila* (fruit flies) [1]. He found that, under controlled settings, male *Drosophila* would mate as frequently as time allowed. Female *Drosophila*, on the other hand, would only mate once or twice, despite the opportunity for further mating. Bateman speculated that this behavioural difference was due to the difference in gamete sizes of the two sexes, with the female's being so much larger and, therefore, more costly. He also suggested this difference would

lead to greater variability in reproductive success between the sexes — that is, females having roughly equal success, but with some males doing very well and other males doing poorly.

Trivers, taking inspiration from Bateman's work, generalised the idea of gamete cost to the idea of parental investment [13]. Parental investment covers any cost that a parent incurs in looking after an offspring, be it in gamete production, gestation or care after birth. As Trivers defines it, 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” ([13], p.139). The definition specifically omits any effort put into attracting mates or competing with members of the same sex for mating opportunities. Other related concepts have been identified, such as parental care (which occurs strictly after birth); see [2] for a detailed review.

The concept of parental investment allows for the explanation of many cases involving sexual selection and the evolution of reproductive strategies. Trivers has used it to explain Darwin's observations of female choosiness and male competitiveness in species where females are the higher investors [13]. He has also used it to explain a parent's ability to vary offspring sex ratios in some species [15], and the period of conflict that will arise between a parent and its offspring during weaning [14]. Others have also found the concept helpful, using it to explain occurrences of infanticide and abortion [7; 8], the greater rate of child homicide amongst stepfathers and boyfriends [4], and the perpetration of rape principally by males [12; 11].

All such cases involve observing a sexual difference in parental investments, and explaining (or predicting) what evolves given such differences. However, this raises the question of how sexual differences in parental investments arise at all. Biologists have suggested several hypotheses. Trivers suggested that pre-existing differences in investment can cause further differences in investments to evolve [13]. Dawkins and Carlisle, in pointing out the faulty reasoning in Trivers' hypothesis, suggested a corrected hypothesis: that the sex that can quit investing first, will [5]. Trivers also suggested the idea that males who were less certain of their parentage would invest less [13]. Finally, Williams noted that the sex that remained with the offspring due to some pre-adaptation would be in a position to evolve parental care [16].

Interestingly, each of these hypotheses also depend on a pre-existing difference between the sexes. Trivers implicitly makes the case that pre-existing differences are likely, since such differences will be passed from species to species — that all that is necessary is a differentiation between the sexes in early evolutionary history [13]. Nevertheless, it is possible that some sexual dimorphism arises entirely anew, independent of existing

sexual differences. If so, it would need to do so by chance, in much the same way that peripatric speciation occurs — that is, with small isolated populations.

Previously [10], we used an ALife simulation to investigate the effect of parental investment on various reproductive strategies – consensual mating, rape and abortion. In this paper, we use the same ALife simulation environment to explore each of the above hypotheses about the origins of parental investment – prior investment, desertion, paternal uncertainty, association with the offspring and chance dimorphism. We set up simulations according to the conditions of each hypothesis, and check how well the hypotheses predictions concur with our results. In some of the simulations, we directly evolve a numerical amount that stands in for parental investment; in other of the simulations, we evolve a period of parental care. As we will see, we find support for all of the hypotheses, barring (unsurprisingly) Trivers’ original, fallacious, hypothesis.

In the next section, we cover the basic design of the simulation. We do so only briefly; for further detail, please see [9]. In subsequent sections, we cover each of the hypotheses in turn. Each such section describes the background, method and results pertinent to the hypothesis that we investigate.

## 1.2 ALife Simulation

**Environment.** The simulation is an agent-based ALife simulation. There are two entities: agents and food. These live on a board which is 25x25 cells in size, and bounded at the edges. The unit of time in the simulation is the cycle. A cycle consists of looping through all the entities currently on the board, and giving each a chance to do something. The simulations here run for 7000, 20,000 or 40,000 cycles. Another unit of time is the epoch, which defines a statistics collection period; an epoch is equal to 110 cycles.

Food is generated each cycle by the system and has a finite life time of 8 cycles on average. In most of the simulations, 50 pieces of food are generated each cycle. Each piece of food has roughly 70 units of health that is absorbed by any agent that eats it.

**Agents.** Agents have a numerical property called health. If the health of an agent falls below 0, it dies. An agent can gain health by eating food, and it will lose health when it moves about or mates. An agent will also gain health by resting, and lose health by continuing to exist (though both of these have a minor effect). Regardless of their health, agents have a maximum age limit of 130 cycles. Further, agents must have a minimum

of 200 health units before they can reproduce.

Agents can perform one of the following five actions: eating, mating, resting, walking and turning. The exception is the simulation used for the association hypothesis, in which walking and turning are replaced with a generic ‘Move’ action (see Section 1.6). Agents choose an action on the basis of observations that they make of their environment. The variables that agents can observe consist of the following: self-health, self-age, self-sex, local food density, local population density and the presence of a mate request from another agent.

To choose an action, an agent passes its list of observations to its genetically inherited ‘decision-maker’ — essentially, a decision tree that is inherited via crossover from an agent’s parents. The decision tree is structured so that each branch node splits on a single observation (an example branch node may be ‘self-health > 0.1’), while each leaf node at the bottom of the tree consists of a probability distribution over the actions an agent can take. Thus, passing the observations down the tree will trigger a single leaf node. Once a leaf node is triggered, the distribution it holds is sampled to determine which action the agent will perform.

**Parental investment.** For this investigation on the origins of dimorphic parental investment, the key agent properties are, obviously, the amount of parental investment,  $pi$ , and the parental investment term,  $it$ . In the simulations reported in this paper, agents can either evolve their parental investment or their investment term, but not both. Each agent stores genetic information about what (or for how long) it invests in offspring, and genes for both male and female investment are stored. A child inherits both these genes from a randomly chosen parent, but only expresses the gene corresponding to its own sex (of course).

These genes are mutated by a mutation variable — itself, stored with each agent. This is so that the system can meta-mutate these mutation variables, allowing for adaptive mutation levels to evolve.

**Statistics.** The main statistics in the following experiments involve averages of  $pi$  and  $it$ . Another important statistic is the action rate, which is defined as follows:

$$\frac{Count_e(a_n)}{\sum_k Count_e(a_k)} \quad (1.1)$$

where  $e$  is a given epoch,  $a_k$  is one of the acts available to agents,  $a_n$  is the act of interest, and  $Count_e(a)$  is a count of the number of times the act  $a$  was performed in the epoch  $e$ . As noted earlier, an epoch is simply a period of cycles in which statistics are gathered. One last important statistic is reproductive success, which is the number of offspring that an agent has.

Usually, average statistics will be collected from a *run set* — that is, a set of runs with identical parameters, that differ only in the initial random number seed. The run sets here consist of 15, 30 or 50 runs, as indicated. Some of the graphs for run sets are displayed with confidence intervals — these use the between run variance of a parameter, *not* the within run variance of the agent population.

### 1.3 Prior investment hypothesis

The first hypothesis we investigate is the one implied by Trivers in his seminal essay on parental investment [13]. Namely, that the sex that commits the most investment has the more to lose — and thus is the sex more likely to evolve further investment. Therefore, if correct, an arbitrary initial difference in parental investments may lead to greater differences of the same kind. In this paper, we call this hypothesis the *prior investment hypothesis*.

While at first this may seem a plausible hypothesis, it was criticised by Dawkins and Carlisle [5], who noted that it involved fallacious reasoning — of the sort used to justify continued spending on a project based on how much has been invested, rather than what future investment will likely return. They used the then topical example of government spending on a supersonic airliner based on past spending, and the fallacy is now often referred to as the ‘Concorde fallacy’.

**Method.** To test the prior investment hypothesis, we set up the simulation as follows. An agent can invest in just one way — that is, by transferring some of its health to its offspring at birth. We call this investment *total parental investment* (or *tpi*). As noted earlier, there is a *tpi* for each sex —  $tpi_f$  and  $tpi_m$  — the genes for which each agent inherits from a randomly chosen parent. The test of the hypothesis is then quite simple: we initially set  $tpi_f > tpi_m$  for all agents at  $t = 0$  (i.e.  $tpi_{f,0} > tpi_{m,0}$ ), and then allow them to evolve. If the prior investment hypothesis holds, then  $tpi_f - tpi_m$  measured late in the simulation should be greater than the same difference at the beginning.

**Results.** Using an initial male investment of zero ( $tpi_{m,0} = 0$ ), we ran two experiments with different initial female investment,  $tpi_{f,0} = 20$  and  $tpi_{f,0} = 100$ . The evolution of the male and female health investments (*tpi*) for these experiments is shown in Figure 1.1(a) and (b) respectively. Clearly, regardless of the initial settings for *tpi*,  $tpi_f - tpi_m$  does not evolve to be greater than it was at first. Indeed, quite the opposite happens — that is, sexually dimorphic investment disappears entirely. We also ran experiments with different initial values for  $tpi_f$  and  $tpi_m$  (ranging from 0

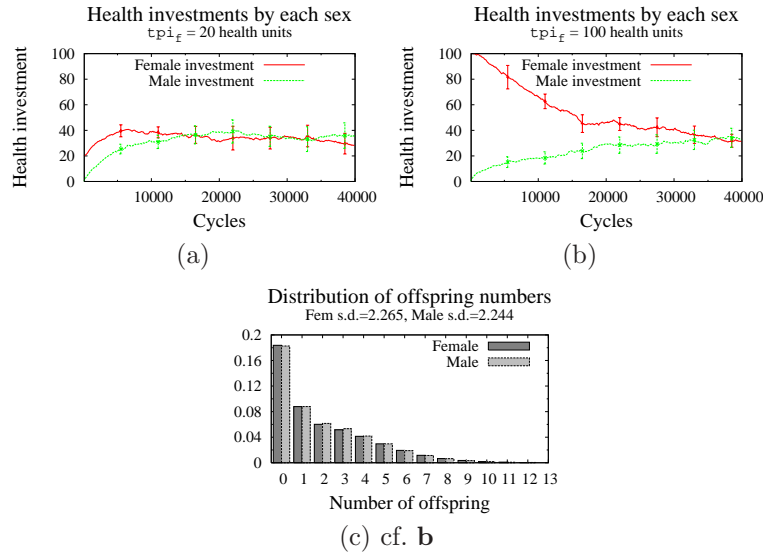


Fig. 1.1 (a) Evolved  $t_{pi}$  made by males and females when  $t_{pi_{m,0}} = 0$  and  $t_{pi_{f,0}} = 20$  and (b)  $t_{pi_{m,0}} = 0$  and  $t_{pi_{f,0}} = 100$ . Also, (c) distribution of reproductive success by sex for the run set shown in **b**. (Average of 15 runs.)

to 100) with the same result.

As noted earlier, Bateman identified a key idea in parental investment theory: that the sex that invests more will evolve to have less variance in its reproductive success [1]. In contrast, we would expect there to be *no* difference in reproductive variability if both sexes invest equally. We check this prediction in Figure 1.1c, which is taken from the last 7000 cycles of the  $t_{pi_{f,0}} = 100$  run set. The graph is a frequency distribution of the number of offspring agents have, split by sex. As we can see, the distributions are near identical. While the distributions are significantly different on a chi-square test, ( $\chi^2 = 161$ ,  $p < 0.001$ ), the Kullback-Leibler (KL) distance between the distributions is negligible ( $7.5 \times 10^{-5}$ ).

In addition to parental investment, we can also see whether any sexually dimorphic *behaviour* is evolving by looking at action rates, as shown in Table 1.1. The top row shows the female minus male difference in action rates that evolves for the  $t_{pi_{f,0}} = 20$  run set, and the bottom row shows the same for the  $t_{pi_{f,0}} = 100$  run set (the numbers in parentheses are the female action rates alone). As we can see, females evolve to eat 82% of the time, while they evolve to mate 16% of the time (the remaining 2% is due to resting). Further, there is little to no dimorphism in both run sets. In fact, there is an initial rapid move toward dimorphism in both eating and

Table 1.1 Female minus male action rates for the prior investment experiments. Female action rates in parentheses.

	Eat	Mate
$t_{pi_{f,0}} = 20$	1.1% (81.4%)	-1.2% (15.3%)
$t_{pi_{f,0}} = 100$	-0.54% (81.7%)	0.54% (15.6%)

mating (not shown), with males mating more, and females instead eating more. This is almost certainly due to the sexual difference in investments at the beginning of the simulations. However, this dimorphism disappears, resulting in no stable dimorphism by the end.<sup>1</sup>

While no stable dimorphism develops for the prior investment hypothesis, we will see an example of stable dimorphism at the end of the next section on the desertion hypothesis.

#### 1.4 Desertion hypothesis

The desertion hypothesis was born from Dawkins and Carlisle's criticism of Trivers' prior investment hypothesis [5]. Dawkins and Carlisle noted that dimorphic investments may evolve when exactly one parent is required to raise a viable offspring. In particular, if one sex has a chance to desert the offspring first, then it will. Dawkins and Carlisle cited parental investment amongst fish as an example of this: in many species of fish, it is the male who looks after the offspring. They suggested that this is because females spawn their eggs first and males fertilize them after — by which time, of course, the female has the opportunity to leave. In contrast, male mammals fertilize female eggs internally, producing zygotes that are stored within the female. Thus, the male clearly has the first opportunity to desert, potentially explaining why *maternal* care (which occurs after birth, of course) is predominant amongst mammals.

**Method.** To test this hypothesis, we allow parents to invest for an evolvable period after birth (the evolvable investment term, or *eit*). For females, we set the minimum *eit<sub>f</sub>* to 5 cycles; in contrast, males have no minimum period (other than 0, of course). The child needs a minimum investment of 32 cycles — so if both parents invest for the same terms, they would

<sup>1</sup>We also ran an experiment in which we set a minimum — non-evolvable — amount that females must make. This simulates investment methods such as gestation, which, once evolved, are difficult to evolve away. We then left each sex free to evolve additional investment. On doing this, we found that females did *not* evolve to make greater additional investments. In some cases, both sexes evolved the same additional investments, while in others, males evolved the greater additional investments.

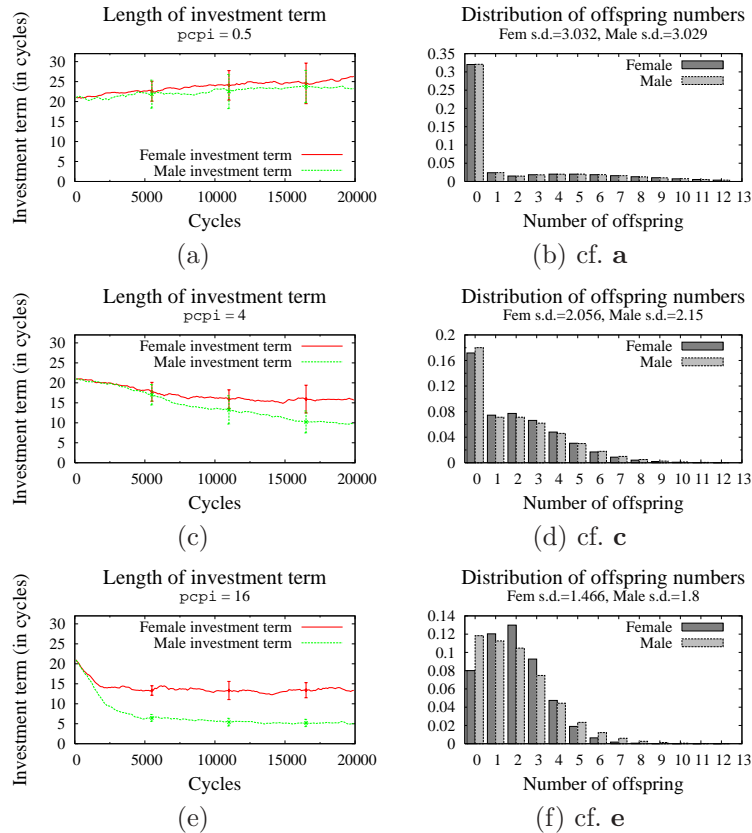


Fig. 1.2 The evolved *eit* for males and females when (a)  $pcpi = 0.5$ , (c)  $pcpi = 4$  and (e)  $pcpi = 16$ . Distributions of reproductive success by sex for the simulations in (b) a, (d) c and (f) e. (Average of 30 runs.)

each invest at least 16 cycles. If one parent quits investing before 16 cycles, the other parent is forced to make up the other parent's investments. We force the remaining investment for simplicity, rather than try to produce environments in which full investment by at least one parent is needed. Finally, we fix the *per cycle parental investment* (or  $pcpi$ ) as a parameter of each run set. In the simulations shown here, the  $pcpi$  takes on one of 3 values: 0.5, 4 and 16 health units per cycle.

**Results.** Figure 1.2 shows the results of our tests of the desertion hypothesis. When the  $pcpi$  is lowest, no dimorphic investments result (Figure 1.2a). In this case, relatively high periods of investment are needed from both parents: each tries to invest for  $\sim 25$  cycles, which results in  $\sim 50$  cycles of



Table 1.2 Female minus male action rates for the desertion experiments. Female action rates in parentheses.

	Eat	Mate
$pcpi = 0.5$	0.38% (59.1%)	-0.52% (29.6%)
$pcpi = 16$	7.5% (71.6%)	-7.2% (20.1%)

combined investment — well above the minimum 32 cycles of investment needed by the child. Thus, the female’s minimum  $eit$  of 5 cycles becomes irrelevant. In the reproductive success distributions for this run set, shown in Figure 1.2b, we can see that no substantial sexual difference exists (KL distance of  $4.8 \times 10^{-5}$ ). Furthermore, there is no sexually dimorphic behaviour evident either (first row, Table 1.2).

For the run set in which  $pcpi$  sits at the higher level of 4 health units per cycle, the result is very different. Here,  $eit_f$  reaches an average of 15 cycles, while  $eit_m$  reaches an average of  $\sim 10$  cycles. Since  $eit_m < 16$ , females must make up the remaining investment, so that females invest for the greater of  $eit_f = 15$  and  $16 + (16 - eit_m) = 22$  — which, of course, is the latter. It is interesting that the minimum  $eit_f$  of 5 cycles can have an effect here. In fact, the average standard deviations of  $eit_m$  and  $eit_f$  (not shown in the graphs) fall between 5 and 7 cycles, allowing the minimum  $eit_f$  to influence the evolution of investments.<sup>2</sup> Note that Figure 1.2d shows that dimorphism in reproductive success begins to develop in this run set.

Finally, in the  $pcpi = 16$  run set shown in Figure 1.2e,  $eit_m$  reaches 5 cycles and  $eit_f$  reaches 15. That is, females come to invest for  $\sim 27$  cycles. This establishes strong conditions for dimorphism, which indeed evolves — as can be seen quite obviously in Figure 1.2f and the bottom row of Table 1.2. This dimorphism is exactly the kind that parental investment theory predicts — that is, that the sex that invests less will evolve to try mating more often. Of course, trying does not equate with succeeding — males (and females) must average 2 offspring in a stable population. Instead, the eagerness of males leads some to greater success, and this in turn causes others to have lesser success; which is exactly what we see in Figure 1.2f.

## 1.5 Paternal uncertainty hypothesis

The paternal uncertainty hypothesis is again due to Trivers [13]. He suggested that males are often in a situation of being uncertain about their

<sup>2</sup>Keep in mind that the confidence intervals in the graphs only use the variance in runs, not the variance in the underlying populations.

parentage, particularly in species where females go through a gestation period. In contrast, uncertain female parentage is very unlikely. In that case, it may pay males to spend less effort on an offspring, and instead spend more effort trying to mate. There is some evidence in humans that paternal uncertainty has an effect on how parents and their families interact. Daly and Wilson report that the mother's family will make comments about how similar the child looks to the father more frequently than reciprocal comments are made by the father's family [3]. Further, Fox and Bruce report that paternal certainty affects how fathers take to their roles as fathers [6].

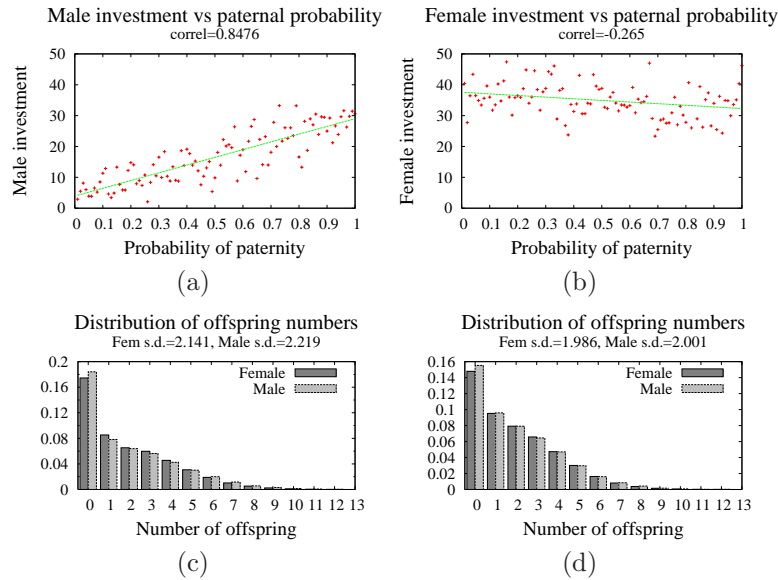


Fig. 1.3 (a) Evolved investments made by males as a function of  $pp$ . (b) as per **a**, but for females. Distributions of reproductive success by sex for (c)  $pp < 0.1$  and (d)  $pp > 0.9$ . (1 run per graph point.)

**Method.** We test the paternal uncertainty hypothesis by fixing the probability of paternity,  $pp$ , as a parameter of the simulation. In particular, females always invest in their own offspring; in contrast, females choose males from the neighbourhood to invest in their offspring according to  $pp$ . At one extreme, if  $pp = 1$  for a simulation, the chosen male is *certainly* the father; at the other extreme, if  $pp = 0$  for a simulation, the chosen male is *never* the father. We set  $pp$  to 101 equally spaced values between 0 and 1 inclusive. As for the prior investment experiments, the parental

Table 1.3 Female minus male action rates for the paternal uncertainty experiments. Female action rates in parentheses.

	Eat	Mate
$pp < 0.1$	3.0% (67.2%)	-3.1% (19.2%)
$pp > 0.9$	0.72% (66.9%)	-0.86% (19.4%)

investments that both sexes make,  $tpi_f$  and  $tpi_m$ , are free to evolve.

**Results.** Figure 1.3a shows the main result of this experiment. Each point in the scatter plot represents the average  $tpi_m$  of the last 1000 cycles (of 7000 total) in a single run. The horizontal axis shows the setting of the  $pp$  parameter for each run, and the vertical axis indicates the investment amount. The result here is clear: the lower the probability of being the actual father, the less males invest in the offspring. Indeed,  $pp$  and  $tpi_m$  have a correlation coefficient of 0.848 ( $t(100) = 15.81$ ,  $p < 0.001$ ). Thus, this result provides strong support for the paternal uncertainty hypothesis.

We can also see how females evolve  $tpi_f$  for different  $pp$  from Figure 1.3b. As  $pp$  increases, and therefore as males invest an increasing amount,  $tpi_f$  falls away slightly. The negative correlation is not large ( $r = -0.265$ ), but is significant ( $t(100) = -2.72$ ,  $p < 0.004$ ). Thus, the more males invest, the more females take advantage by investing less.

To assess the level of dimorphism (in behaviour and reproductive success) that evolves in these runs, we take the runs in which  $pp < 0.1$  as one group and  $pp > 0.9$  as another. The former should exhibit more dimorphic behaviour, while the latter should exhibit less. Figure 1.3c and Figure 1.3d shows the reproductive success distributions for the last  $\sim 1200$  cycles of runs with  $pp < 0.1$  and  $pp > 0.9$ , respectively. We can see that there is a slight dimorphism evident in the  $pp < 0.1$  runs (KL distance of 0.0011) that is not evident in the  $pp > 0.9$  runs (KL distance of 0.00019). More tellingly, we can see a reasonably strong behavioural dimorphism in Table 1.3 for the  $pp < 0.1$  runs, that is much reduced in the  $pp > 0.9$  runs.

## 1.6 Association hypothesis

The association hypothesis or, more generally, the pre-adaptation hypothesis was suggested by Williams [16]. He noted the perhaps obvious point that if only one sex remains in the vicinity of the offspring after birth — due to some pre-adaptation of that sex — then that sex has the opportunity to evolve parental care, while the other sex does not.

**Method.** As it stands, the association hypothesis is almost tautological.

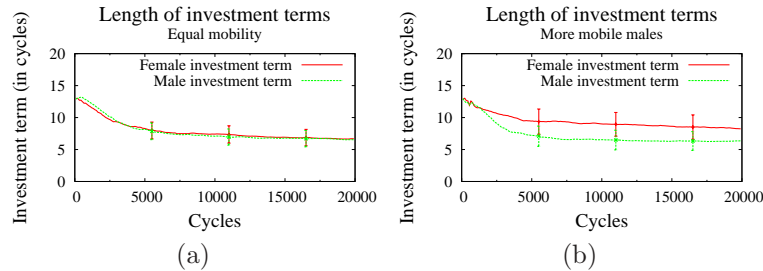


Fig. 1.4 The evolved after birth investment terms for both males and females for (a) no sex differences and (b) males as the more mobile sex. (Average of 50 runs.)

However, this need not be so: the sex that does *not* remain with the offspring — which we will take to be the male in these experiments — could evolve to return every so often to make parental investments. There is no a priori reason why males cannot continue investing. Nevertheless, males will find it *harder* to invest in offspring. ‘Harder’ here simply means that males have to do more to invest at the same rate as females. In this case, it is not immediately obvious that females will invest more than males, though we would expect them to do so since they find investment easier.

We choose to test this form of the hypothesis by having a non-evolvable ‘Move’ action that causes males to move about more actively. Specifically, males move about randomly in a 9x9 neighbourhood with 0.6 probability each cycle, while females move about randomly in a 3x3 neighbourhood with 0.2 probability each cycle. In addition, we established that parental investments have a certain ‘efficiency’, dependent on the distance from the child. That is, the closer one is to a child, the more of one’s investment reaches the child. The function of efficiency,  $e$ , over distance,  $d$ , that we used is a simple linear inverse function of distance from the parent:  $e = 1 - \frac{d}{20}$  if  $d < 20$  and  $e = 0$  otherwise. The distance is the minimum number of cells in either the horizontal or vertical direction.

Similar to experiments in previous sections, the investments are in the form of per-cycle investments after birth. Here,  $pcpi = 8$  and agents are free to evolve the term for which they invest (the *eit*).

**Results.** Figures 1.4a and b show the results of 2 run sets, the first in which the ‘Move’ action is the same for both sexes, and the second in which the ‘Move’ action makes males more mobile. The graphs show the *eit* for both sexes. In the first graph, no dimorphism evolves — as we would expect. In contrast, the second graph shows that females — the sex that can invest more efficiently — evolve to invest for longer periods.

Surprisingly, the degree of behavioural dimorphism that evolves is very

Table 1.4 Female minus male action rates for the association experiments. Female action rates in parentheses.

	Eat	Mate
<b>Equal mobility</b>	0.20% (68.0%)	-0.18% (23.8%)
<b>More mobile male</b>	1.1% (66.2%)	-1.1% (25.2%)

slight. The bottom row of Table 1.4 shows that a difference of only 1% in action rates evolves — in contrast to experiments in previous sections that showed differences of between 3% and 7%. Further, dimorphism in reproductive success (not shown) is not evident (KL distance of  $6.6 \times 10^{-5}$  for the more mobile male run set).

### 1.7 Chance dimorphism hypothesis

All of the above hypotheses on the evolution of sexual dimorphism assume that there is a pre-existing sexual difference. But there may be cases in which there is no pre-existing difference or, perhaps more likely, that an existing difference is not sufficient to cause the evolution of further dimorphism. Trivers suggested that the sexes differentiated very early on due to positive selective pressure acting on gametes whose sizes fell in the tails of the normal curve [13]. That is, smaller, mobile, gametes would be selected for since they can fertilize other cells more easily, while larger, immobile, gametes would be selected for since they increase the probability of a viable offspring. In contrast, those with intermediate sizes would not fare so well. Trivers does not seem to regard this process as occurring anew in new species, but rather occurring amongst progenitor species, from which dimorphism is inherited.

However, perhaps it is possible, as Gould might hold, that sexual differences in parental investment can arise by chance. If a chance difference in investments persisted for long enough, the sexes may adapt to the difference. This could then ‘lock them in’ — that is, chance reductions in dimorphic investment could cause agents to become less fit, and thus be selected against. We would expect such events to be most likely amongst small populations, since the genetic variance *within* such populations will be small, while the genetic variance *between* such populations will be large.<sup>3</sup>

**Method.** To see if dimorphism may arise at all, we run several runs in which the sexes are initially identical, and then see whether substantial dimorphic investments ( $|eit_f - eit_m|$ ) and behaviour can develop. Further, to discover if the size of the population has an effect on the frequency with

<sup>3</sup>This is similar to the argument supporting peripatric speciation.

Table 1.5 Averages and standard deviations of degree of dimorphism ( $dd$ ) for runs of differing population sizes. (Average of 50 runs.)

Avg stable pop'n size	Mean dimorphism ( $dd$ )	S.D. of $dd$
237	$\mu = 44.32$	$\sigma = 83.96$
409	$\mu = 29.19$	$\sigma = 54.98$
648	$\mu = 9.25$	$\sigma = 11.91$
901	$\mu = 11.19$	$\sigma = 17.12$

which dimorphism develops, we run the simulations with different sized populations — which we achieve by regulating the food supply. To assess the degree of dimorphism,  $dd$ , for a single run, we take the mean  $|eit_f - eit_m|$  in that run, and divide by the pooled standard deviation of  $eit_f$  and  $eit_m$  within that run; this is so as to counter the run to run differences. In essence,  $dd$  is the number of standard deviations of difference between  $eit_f$  and  $eit_m$ .

**Results.** Figure 1.5 summarises the results of run sets, each with different average population sizes. The table shows the mean  $dd$  for a run set with a given population size (along with the standard deviation). The first thing to note is that dimorphism evolves quite regularly. If we focus on those cases in which there are 3 standard deviations or more of difference (i.e.  $dd \geq 3$ ), we note that dimorphism results in half or more of all cases (not shown). Further, there seems to be an inverse correlation between the size of the population and the average  $dd$  that evolves.<sup>4</sup> There also seems to be an inverse correlation between the variance of the  $dd$  and population size.

## 1.8 Conclusion

We have explored various hypotheses on the origins of sexually dimorphic investments through simulation, and found support for those that we would expect to be correct. Our simulation results concur with the view that the prior investment hypothesis is wrong, given initial sex differences in investments (and also minimum sex differences in investments). We found strong support for the desertion hypothesis and for the paternal uncertainty hypothesis. While our results also agreed with the association hypothesis, the level of dimorphic behaviour and reproductive success in these experiments was lowest. Finally, we had little difficulty in finding simulations that produced dimorphism by chance, and confirmed that smaller populations do indeed lead to greater levels of dimorphism.

<sup>4</sup>The last run set here defies this trend, but runs that we further tested, using larger populations, continue the correlation.

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