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**ON THE RELATIVE IMPORTANCE OF HAPLO-DIPLOIDY, ASSORTATIVE MATING
AND SOCIAL SYNERGY ON THE EVOLUTIONARY EMERGENCE OF SOCIAL BEHAVIOR**

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ABSTRACT. - Advances in multiagent simulation techniques make it possible to study more realistic dynamics of complex systems and allow evolutionary theories to be tested. Here I use simulations to assess the relative importance of reproductive systems (haplodiploidy vs. diploidy), mate selection (assortative mating vs. random mating) and social economics (pay-off matrices of evolutionary games) in the evolutionary dynamics leading to the emergence of social cooperation in the provision of parental care. The simulations confirm that haplo-diploid organisms and organisms mating assortatively have a higher probability for fixing alleles and require less favorable conditions for their fixation, than diploids or organisms mating randomly. The simulations showed that social behavior was most likely to emerge a) when the cost for parental investment was much lower than the benefits to the offspring, b) when cooperation improved synergistically the fitness of offspring compared to the corresponding egoistic behavior and c) when alleles coding for altruistic or social behavior could be rapidly fixed in the population, thanks to mechanisms such as haplo-diploidy and/or assortative mating. Cooperative social behavior always appeared if sociality conferred much higher fitness gains compared to non cooperative alternatives suggesting that the most important factors for the emergence and maintenance of social behavior are those based on energetic or efficiency considerations. The simulations, in congruence with the scant experimental evidence available, suggest that economic considerations rather than genetic ones are critical in explaining the emergence and maintenance of sociality.

Key Words: evolution, haplo-diploidy, sex, strategy, polyploidy, assortative mating, sociality, economy

INTRODUCTION

How social behavior arrived through evolution is still an unsettled aspect of evolutionary theory. A large amount of literature exists on the role of game theoretical mechanisms applied to explain mutualism and thus of sociality, of genetic mechanisms such as haplo-diploidy which promote genetic relatedness favoring kin-selection, and economic considerations in explaining the emergence and maintenance of social behavior, which I will not be able to review here (see review of Crespi and Choe, 1997 for example). But none of these studies, to my knowledge, tackles the relative importance of these aspects in modulating the evolution of social behavior.

Haplo-diploidy or arrhenotoky is known as the reproductive mechanism by which unfertilized eggs produce haploid males whereas fertilized ones produce diploid females. Haplo-diploidy is common among social insects and thus has been proposed as a mechanism which facilitates the evolutionary emergence of social behavior, at least among Hymenoptera, thanks to the fact that it produces an asymmetric genetic relatedness between daughters and sister, increasing genetic relatedness among sisters, and thus favoring altruistic behaviors (Hamilton, 1964; West-Eberhard, 1975). However, actual field data has proved difficult to explain using this theory (see introduction in Reeve, 1993 and review in Crespi and Choe, 1997; Jimenez, 1998, for example).

Assortative mating favors genetic relatedness among the offspring. Assortative mating can either be passive, i.e., population viscosity favors reproduction among spatially proximate individuals, or active, i.e., individuals chose their mates based on similar phenotypic traits which reflect similar genes. In both cases it produces more genetically related interbreeding populations. Assortative mating has been shown to affect the evolutionary dynamics of sexual organisms significantly (Davis, 1995; Jaffe, 1999; 2000; Kondrashov and Kondrashov, 1999; Dieckmann and Doebeli, 1999.) and may thus be a force to take into account when studying the emergence of social behavior.

Favorable pay-off matrices in game theory may also been invoked as facilitating the emergence of social behavior (Maynard-Smith, 1976). This argument, presented in thermodynamical terms, predicts that social behavior has to be more efficient in the exploitation of the habitat, in defense, or in any feature related to fitness, which appropriately measured should be reflected in the use of energy, than the equivalent individual behaviors (see review in Jaffe and Fonk, 1994 for example). That is, social behavior should increase the fitness of cooperating organisms.

Here I want to answer two questions: 1- Do these features together explain the emergence of social behavior better than each of them alone ? 2- Are some of them more relevant than others in favoring the evolutionary dynamics for the fixation of altruistic alleles ?

A simulation model was developed to allow comparisons between different sexual

reproductive systems in respect to their relative advantages regarding the three criteria outlined above. A simulation model was chosen for this task due to the complex nature of the aim and due to the fact that agent based simulation of evolution has shown to be very useful in pinpointing the bottlenecks and relative importance of the various factors affecting evolution (Ruelle, 1991; Levin et al., 1997). The model for the evolution of organisms had been validated extensively before (Jaffe, 1966-2000) and assumes many simple organisms composed of up to 20 genes providing a finite genotype-phenotype search space of 10^{20} . This model, although still far simpler than real evolution, is significantly more complex than those assumed in models of genetic algorithms or of artificial life. Due to the complexities of the present model, it had to be validated in order to have some confidence in its results. This was done by producing predictions related to the odds for the emergence of genetic resistance to pesticides in sexual and asexual organisms, an area where sufficient experimental data is available. The results showed that the increased complexity of the model paid off, as its predictions were more accurate and less contradictory than those of alternative models in explaining the available experimental data (Jaffe *et al.*, 1997).

Here, for modeling purposes, the classical haplo-diploid strategy was decomposed into two components, each specified by the alleles of a gene: the ploidy number of individuals and the inheritance mechanism. Two alternative inheritance mechanisms were modeled: Sexual-Asexual Strategy (SAS), in which males are produced by unfertilized female eggs and females are produced only after sexual reproduction; and Sexual Strategy (SS) where both females and males are produced sexually. SAS males were always haploid, whereas SAS females could be haploid or diploid. Thus, 4 possible reproductive strategies could be simulated: SAS with haploid males and haplo- or diploid females, and SS with haplo- or diploid males and females. For example, a SAS haploid was an organism in which all individuals were haploid and where the males inherited genetic material only from their mothers whereas females inherited a mix of genetic material from both parents. The ploidy number in SS was the same for males and females. These strategies were tested for their survival properties and for their effect on the emergence of altruistic or cooperative behavior in parental care.

METHODS

The numerical simulation model Biodynamica (Jaffe, 1995) was used. This agent based adaptive Monte Carlo model, was tailored as closely as possible to living organisms. It simulates a population of virtual organisms, each carrying a number of genes. The genetic characteristics of the organisms were assigned at random among the individuals of the initial population, which then varied (i.e., suffered variation and selection) according to the constraints of a five-step transformation process (see below). The alleles of each gene coded for specific phenotypic characteristics of the organisms subjected to selection as given in Table I. Two situations were modeled: Organisms with low, and with high genetic complexity. In both

cases organisms had 13 genes, but when low complexity was simulated, only the two genes selected for study had allelic variance, and the rest of the genes had default values for their alleles (Table I). Simulation of high genetic complexity allowed to study the effect of strong genetic drift and for dynamic interactions among evolving genes. The five transformation steps consisted of the following:

Mate selection: Females chose males either randomly or based on assortative mating criteria (for other mate selection strategies see Jaffe, 1998; 1999). In assortative mating, females mated with the male which had the allelic configuration most similar to hers. Females not finding any male after randomly screening a given number of individuals (defined by gene 5 in Table I) did not reproduce during that time step.

Reproduction: Mated females produced offspring according to their phenotypically expressed clutch size, transmitting their alleles to the offspring according to their ploidy number and their inheritance mechanism (either SS or SAS). Each parent provided at random alleles to the newborn with the probabilities indicated in Table II. Of the possible reproductive strategies studied, only SAS with haploid females does not exist in nature to my knowledge. It was included in order to maintain the symmetry of the rationale and hoping to eventually find reasons why SAS with haploid females do not exist in nature (see Jaffe, 1996; Jaffe, 1999).

Variation: Randomly selected genes mutated, changing their allelic value at random according to the genetically determined mutation rate (gene 13 in Table I), or at the default average value of 1 mutation ever 25 genes in newborns, which was close to the optimal mutation rate for this model (Jaffe, 1996; Jaffe et al., 1997). The existence of genes determining mutation rates have been proposed (LeClerc et al., 1996 for example) and can be simulated here.

Phenotypic expression: As mechanisms for allelic dominance are poorly understood, only allelic suppression, corresponding to genetic dominance in classical Mendelian genetics, was simulated, as is common in genetic algorithms (Goldberg, 1989). That is, only one allele chosen at random was expressed phenotypically in each loci (which represents a complete gene) in diploids, whereas the only allele present in each loci was expressed in haploids. The phenotype expressed depended on the value of the allele as indicated in Table I.

Selection: The model did not assume any simplified expression of fitness but reproduction and individual survival were decomposed into different aspects for selection to act. Individuals were excluded from the population when any of the following criteria was true:

1- Their age exceeded their potential maximum life span as expressed by alleles of gene 1 (Table I).

2- They were randomly selected by density dependent criteria. The number of individuals killed at random increased the closer the population was to the optimal population size (500 individuals, unless stated otherwise). This allowed simulations to maintain population sizes at levels manageable by the computer.

3- Individuals not expressing the resistant allele of genes 6 and 7 (Table I) were killed with a probability which varied randomly each time step between 0 and 0.9. This part simulated natural selection acting on genetically weak individuals (see Jaffe et. al., 1997)

All three criteria copy known mechanisms for population regulation and were always implemented together.

No linkage between loci was built in. Sex of offspring was determined randomly at a 50/50 ratio. The population endured the five-step transformation, at each time step, representing one reproductive cycle. Generations overlapped as each female reproduced independently. Thus, one time step corresponded, under the life history traits simulated here, approximately to 0.2 generations (i.e. 5 time steps corresponded in average to one generation). The exact genetic composition of the population was plotted at each time step, with the actual number of surviving individuals. Thus I could assess when and if the population reached a stable population size, and at the same time monitor the genetic composition of the population at each time step.

Simulation aimed at assessing the effect of selection on the allelic distribution of a given gene in a single interbreeding population. For example, alleles coding for different parental investment strategies were assigned at random but uniformly among the first individuals. The simulation was started and the frequency in the population of the various alleles was monitored for each time step. In experiments designed to assess the evolutionary stability of certain strategies, the initial population had individuals, all with the same allele for that strategy. After 20 time steps, mutant alleles coding for different strategies were allowed to appear, and the frequency of the two alleles was monitored for at least a further 400 time steps or until the mutant allele displaced the other.

For the study of the evolution of social behavior, a theoretical game was developed. It was based on the eventual evolution of social behavior through development of altruistic cooperative care of the offspring or extended parental care (Alexander, 1974; Queller, 1994; Crespi and Choe, 1997). As all known eusocial or truly social species developed cooperative care of the young prior to reaching full eusociality (Michener, 1974; Wilson, 1976), the game was developed to compare the evolutionary dynamics of 5 parental investment strategies. Brood care could be provided by both sexes or by only one of them (according to alleles of gene 12 in Table I). The strategies for brood care, coded by the alleles of gene 10 (Table I),

were designed as idealized strategies, whose mixes cover most of the behaviors based on parental investment, known to exist in nature (see Wilson, 1976 for example). These were:

No care: Parents did not invest in offspring. (This probably represents an extreme situation as even in species with no parental care, mothers invest in their offspring prior to laying eggs or giving birth)

Communal care: Parents invested equally in all offspring of the population, irrespective of genetic relationships. This strategy models extreme alloparental care. Alloparental care is fairly common (for example among coleoptera: Scolitydae and Curculionidae, and communal wasps).

Open care: Parents invested half their available energy in their own offspring and half in all other offspring. This represents a mix of alloparental care with selfish care (for example social primates, ungulates and wasps).

Opportunistic care: Parents invested only in their own offspring, but their offspring received half of the care from open or communal parents. This strategy appears to be used by species breeding in communal breeding sites (for example among birds, sea lions, elephant seals).

Closed care: Parents invested only in their own offspring and their offspring could not receive care from any other adult. (for example digger wasps, scorpions, dung beetles)

Each organism possessed an additional gene defining the “degree of parental investment” (gene 11 in Table I) whose allele coded for the amount of energy spend in caring for the brood . Each parent investing in offspring suffered a cost to its fitness which was directly proportional to the “degree of parental investment” multiplied by the cost/benefit ratio of investment. The cost/benefit ratio of parental investment was constant for each simulation and determined the ratio between the cost in fitness to the parent making the investment and the benefit in increased fitness to the offspring receiving the care. The increased fitness of offspring receiving parental care was directly proportional to the “degree of parental investment” only.

A constant simulating the benefit of sociality (“social synergy”) determined the amount of synergy achieved by social behavior. This “social synergy” increased the increase in fitness the offspring received from caring adults if the care was communal, and half that amount if the care was open, but not if the care was opportunistic or closed. That is, I assumed that parental investment was more efficient with cooperation. This assumption can be illustrated taking as an example two extreme situation of brood care. More time dedicated to caring the brood will reduce the odds of parasites or predators killing the offspring. If one parent invest 50% of its time to care for its brood, it will leave the brood unattended 50% of the time, and the odds of losing the brood are $p = 50 * k$, where k is a proportionality constant. If two parents attend their brood communally, each one investing 50% of their time in brood care, the brood may be

protected 100% of the time, reducing the odds of losing their brood to zero with the same cost to parents. In this example the value for “social synergy” is $50 \cdot k / 0 = \text{infinite}$ for $k > 0$. A “social synergy” value of 1 indicates no advantage of communal care over egoistic parental investment.

All data presented here are the average result of at least 200 simulations.

RESULTS AND DISCUSSION

In order to assess the effect of diploidy and haplo-diploidy on the likelihood of altruistic genes being fixed in a population, “gene selection” experiments were performed. The simulations compared the ability of each of 5 alleles, coding for different parental care strategies, in displacing the others. These experiments were performed with haplo-diploid and pure diploid organisms using either assortative mating or random mating. Simulations of extreme situations gave the expected results. That is, for values of cost/benefit ratios of parental investment greater than 1 (i.e. the cost to the parent is much greater than the benefit to the offspring), alleles coding for no parental investment displaced all others. Values of social synergy less than 1 made that alleles for egoistic (opportunistic and closed) parental investment displaced all others. Simulations using values of cost/benefit less than 1 and of social synergy greater than 1, gave interesting results (Fig 1). Each combination of reproductive system and mate selection strategy produced a different evolutionary dynamics of the allelic frequency for the gene coding for parental care. In all cases, the extreme strategies, i.e. communal care and closed care, displaced the intermediate strategies for parental investment. The allele coding for closed care rapidly increased its frequency in populations using random mating in both haplo-diploid and diploids, but in the long term (200 time steps) alleles coding for communal care became the most frequent, except in diploids using random mating. Strategies using assortative mating fixed alleles coding for communal care faster than those using random mating. This dynamic was influenced by the cost-benefit ratio of parental investment and by the amount of synergy social behavior could achieve (Fig 2-3). That is, at high cost/benefit ratios, alleles coding for closed care were more likely to be fixed in the population, whereas high values of social synergy favored communal care. Assortative mating favored the invasion of alleles for communal care at higher cost/benefit and lower social synergy values than random mating. Also haplo-diploidy favored the invasion of communal alleles at higher parenting costs and lower social synergy values than pure diploids, but to a smaller degree than assortative mating. Thus, populations of haplo-diploid organisms using assortative mating could fix alleles coding for communal care at about twice the cost/benefit ratio for parental investment and about half the social synergy value than diploid organisms mating at random.

These results were affected by the genetic complexity of the simulated organisms. In more complex organisms, intermediate strategies for parental care became more frequent

(Table III). Assortative mating was less successful in accelerating the fixation of advantageous alleles in simulations using genetically more complex organisms. This effect of genetic complexity was partly due to the increased genetic drift suffered by these populations. Simulations with larger population sizes showed less genetic drift and the advantage of assortative mating increased again (Table III, last row). Other explanations for the susceptibility of the evolutionary dynamics on genetic complexity when simulating non-random mating may exist, such as the “evolutionary wanderlust” reported by Miller and Todd (1994). That is, assortative mating fixes rapidly the genetic composition of populations, and thus, in rough fitness landscapes, will drive the population to the nearest fitness peak, which is not necessarily the optimal in respect to all the fitness peaks present.

Analytical models of haplo-diploidy as related to the evolution of social behavior, have proposed some interesting predictions than can be tested with the present model. Specially, the protected invasion hypothesis (Reeve, 1993), based on differential probabilities of loss of alleles due to genetic drift, postulates that haplo-diploidy should favor female versus male parental investment. The present model confirmed that this effect was real. Although investment by both parents was always more successful than either male or female parental investment, if simulations allowed for parental investment of only one sex (either female or male), female parental investment showed to be more successful than male parental investment among haplo-diploids mating randomly but not among diploids. This preference was evident at the beginning of simulations (Fig 4), disappearing after approximately 70 time steps. Other factors were much more important in determining which sex was more likely to engage in parental investment. For example, if the cost/benefit ratio for both sexes was the same and the genetic dominance of the alleles coding for parental investment was the same for both sexes, the sex with the highest variance in reproductive success fixed the alleles for parental care fastest. That is, in the present model males had a greater variance in reproductive success when simulation random mating, as they could mate more than once per time step (females mated only once per time step), and had much larger variance when simulating assortative mating, which also increased the probabilities of fixing male parental care alleles (HD-A and D-A in Fig. 4). If the cost of reproduction differed between sexes, the sex with the highest cost had a higher probability of fixing alleles for parental investment (Over 600 simulations with 30 different settings, data not shown). These result are compatible with what is known for life history evolution (Roff, 1992), and has little to do with genetic dynamics, and thus, this aspect was not studied further (but see Roff, 1992). These results focus on the dangers of over-simplification of complex biological processes (Caswell and Weeks, 1986; Cressman, 1988; Levin et al., 1997), as several factors affect the evolutionary dynamics and the relevance of each factor has to be assessed in its relation to others.

CONCLUSIONS

Simulations showed that Haplo-diploidy drives evolution with a faster dynamics than pure diploidy, confirming that the simulations are in agreement with the existing literature (Mable and Otto, 1998). This special ability for fast adaptation of a complex assemblage of genes is a general feature of haplo-diploidy, not restricted to the evolution of social behaviors, due to the increased exposure of alleles in haploid males, explaining why haplo-diplodization technologies improve crop selection (Goldringer et al., 1996) and why haplo-diploid populations establish faster resistance alleles than diploid-diploid ones (Caprio and Hay, 1995). The success of haplo-diploidy in simulated gene selection trails with organisms of low complexity is due to advantages of female genes for generating uniparental males (Bull, 1983), showing that the results of the simulations are in agreement with existent data and theory. Thus, haplo-diploidy may explain the frequent occurrence of eusocial species among the Hymenoptera, but due to different reasons than those proposed by Hamilton's kin-selection theory (Hamilton, 1964).

The model used do not allow to study kin-selection directly, but assortative mating increases genetic relatedness in the population, favoring kin-selection. The results suggest that assortative mating could be a strong driving force favoring emergence of social behavior. Assortative mating is known to be a strong evolutionary driving force (Davis, 1995; Jaffe, 1998) and is a more general mechanism than kin selection, allowing for the maintenance of altruistic behavior even in the absence of close genetic relatedness. Therefore, social behavior among social wasp species with low genetic relatedness (Queller et al., 1988; Gadadkar, 1990; 1991) could be favored by assortative mating for behavioral features relevant to social behavior. Experimental data on mating behavior could thus be used to refute or support the present theories. The hypothesis favored by the results presented here is congruent with both, the prevalence of social behavior among haplo-diploid organisms such as the Hymenoptera, and the emergence of cooperative behavior among diploid organisms, such as the Isoptera for example (see also Crespi and Choe, 1997). A testable assessment of the importance of assortative mating in the evolution of social behavior, is that species with social behavior should have non-random mating strategies, which seems to be the case at least for human females (Buss, 1989; Jaffe and Chacon, 1995). Assessment of equivalent data for other social and sub-social species urgently needed.

The results suggest that economic considerations (the cost-benefit ratio of parental investment, the amount of synergy achieved by social behavior) are the most important factors explaining the emergence and maintenance of social behavior, followed with decreasing importance by assortative mating, haplo-diploidy, and the protected invasion hypothesis. Interestingly, the model revealed the obvious but neglected fact that social behaviors which

provide no social synergy in increasing the fitness of the offspring are unlikely to emerge in biological evolution. Social behavior should emerge in evolution when cooperation or altruism improves synergistically the fitness of offspring compared to the corresponding egoistic behavior, and when alleles coding for social behavior can be rapidly fixed in the population, by strategies such as haplo-diploidy, assortative mating, and probably others (Simon, 1990 for example). The social synergy needed to boost the likelihood for fixing social behaviors seems to be very low as the threshold value of approximately 4 (Fig 3) is very low compared to the synergy value estimated in the example given in the introduction. The results of these simulations suggest that social behavior is unlikely to emerge when the cost to the parents providing investment is much higher than the benefits received by the offspring, favoring egoistic varieties of parental investment instead. Generalizing this idea, we might postulate that social behavior in general emerges and is maintained when the economics of sociality provides larger fitness gains compared to that of individual solutions. Experimental results seem to support these predictions. Among examples of mutualistic interactions between Lycaenid (Lepidopera : Lycaenidae) larvae and ants, cooperation is much more common than exploitation (Osborn and Jaffe, 1977). No kin-selection argument can be given for explaining social cooperation between these non related taxa, suggesting that rather economic considerations may explain the frequency of those cooperation's. Other evidence for the importance of social economics are measurements comparing the energetic efficiency between isolated individuals and social aggregations or between small and large societies. These measurements showed that sociality increases the energetic efficiency in ants (Fonk and Jaffe, 1996), in termites (Muradian et. al., 1999) and in human settlements (Cabrera and Jaffe, 1998), supporting the results of the simulations presented here.

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Table I : Genes used in the simulations and its possible alleles. Genes with no variance had one allele with the default value.

Gene	Alleles	Phenotypic expression
1	11	Maximum life span: ranging from 0 to 10 time steps. Default : 10 time steps.
2	11	Maximum clutch size from 0 to 10 offspring. Default : 3 offspring / female.
3-4	6-6	Minimum reproductive age for males and females coding for ages from 0 to 5 time steps. Default : 1 time step.
5	90	Number of males screened by females searching potential mates ranging from 1 to 90. Default : first male encountered for random mating, and 20 males for assortative mating.

6-7	11-11	Resistance to two different biocides. Allele 0 was resistant where other were susceptible. Default : 0
8	2	Inheritance mechanism, either SAS or SS.
9	2	Ploidy, either haploid or diploid.
10	5	Strategy used for parental investment. Default: no investment
11	11	Degree of parental investment. Default: 0
12	3	Sex providing parental investment. Default: both sexes.
13	10	Rate for random mutations, ranging from one mutation every 1 to 10×10^6 genes in every newborn, increasing in logarithmic steps. Default: average of one mutation every 25 genes.

Table II: Probability for inheritance of at least one allele:

Inheritance mechanism	SS	SS	SAS	SAS	
Ploidy number : Females		1	2	1	2
Males	1	2	1	1	
Maternal alleles to daughter :		0.5	1	0.5	1
Maternal alleles to son :		0.5	1	1	1
Paternal alleles to daughter :		0.5	1	0.5	1
Paternal alleles to son :		0.5	1	0	0

Table III: Percentage of alleles coding for the different parental investment strategies, in simulated populations, when simulating gene selection of genetically 'simple' and 'complex' organisms at time step 200. Cost/benefit = 0.3, Social synergy = 4. Simple organisms had allelic variance only for genes 10 and 11 in Table I, whereas those with high genetic complexity had allelic variance for all genes in Table I, except gene 8 and 9.

Experiment	Strategy	% Communal	% Closed	% intermediates
Simple	D-R	49	15	36
Complex	D-R	45	13	42
Δ %		-08	-13	+17
Simple	HD-R	58	13	29
Complex	HD-R	53	09	38
Δ %		-09	-31	+31
Simple	D-A	79	12	09
Complex	D-A	50	26	24
Δ %		-37	+117	+167
Simple	HD-A	90	03	07
Complex	HD-A	56	24	20
Δ %		-38	+700	+186
Complex ***	HD-A	70	09	21

*** optimal population size = 1000, else = 500

Δ % = ((Complex – Simple) / Simple) * 100

Figure 1: Temporal dynamic of the relative frequency of alleles (frequency) of the gene coding for strategy of parental investment for haplo-diploids with random mating (HD-R), haplo-diploids with assortative mating (HD-A), Diploids with random mating (DP-R) and diploids with assortative mating (DP-A). Values for social synergy = 3, degree of investment = 50 % of fitness, cost/benefit ratio = 0.3. Simulations were for gene selection of simple organisms as defined in Table V.

Figure 2: Effect of the cost/benefit ratio on the relative frequency of alleles coding for communal investment. Values for social synergy = 4. Results were assessed after 200 time steps. Else as in Fig. 1

Figure 3: Effect of the social synergy on the relative frequency of alleles coding for communal investment. Values for cost/benefit ratio = 0.3. Else as in Fig. 2

Figure 4: Frequency of alleles coding for male parental investment in simulations of gene selection when 8 different allelic combinations competed for survival. That is, male investment by haplo-diploids (HD) and diploids (D) using either random mating (R) or assortative mating (A). (The frequency for alleles coding for female parental care are 100% minus that shown for males and are thus not shown).





