Human origins and the transition from promiscuity to pair-bonding

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A crucial step in recent theories of human origins is the emergence of strong pair-bonding between males and females accompanied by a dramatic reduction in the male-to-male conflict over mating and an increased investment in offspring. How such a transition from promiscuity to pair-bonding could be achieved is puzzling. Many species would, indeed, be much better off evolutionarily if the effort spent on male competition over mating was redirected to increasing female fertility or survivorship of offspring. Males, however, are locked in a "social dilemma," where shifting one's effort from "appropriation" to "production" would give an advantage to free-riding competitors and therefore, should not happen. Here, I first consider simple models for four prominent scenarios of the human transition to pair-bonding: communal care, mate guarding, food for mating, and mate provisioning. I show that the transition is not feasible under biologically relevant conditions in any of these models. Then, I show that the transition can happen if one accounts for male heterogeneity, assortative pair formation, and evolution of female choice and faithfulness. This process is started when low-ranked males begin using an alternative strategy of female provisioning. At the end, except for the top-ranked individuals, males invest exclusively in provisioning females who have evolved very high fidelity to their mates. My results point to the crucial importance of female choice and emphasize the need for incorporating between-individual variation in theoretical and empirical studies of social dilemmas and behaviors.

food-for-mating | self-domestication

There are many characteristics that make us a "uniquely unique" species, including those related to morphology, ecology, development, and life history as well as sexual, social, cognitive, linguistic, and cultural traits and abilities (1–4). Both ultimate and proximate mechanisms that were driving their emergence and evolution in hominins are the subject of intensive research efforts and numerous controversies. Recent influential theories link the appearance of some of the unique human features to a major transition in life history strategy that transformed the social structure of early hominins from promiscuous groups to multimale/multifemale groups with strong pair-bonding (4–9). After the new mating system had evolved, a number of subsequent evolutionary transitions became possible. In particular, pair-bonding served as a preadaptation to parental partnership based on the division of labor, which was necessary to offset the disproportionally high costs of raising human children (because of their large brain and delayed maturity). Pair-bonding allowed children to recognize their fathers (and vice versa) on a reliable basis, and subsequently, it led to the emergence of a new type of family that integrated three generations of individuals of both sexes. Recognition of kinship networks simplified the evolution of within-group cooperative behavior, including alloparental care. It also allowed for between-group alliances taking advantage of the bonds between females transferring to other groups and their fathers and brothers remaining in the natal groups.

How such a transition from promiscuity to pair bonding could be achieved is puzzling (4–6, 10–13). The classical explanation of monogamy in primates—that females' dispersion across a landscape forces males to associate with individual females (14)—does not work for group-living species with strong within-group dominance hierarchies and high-ranked males largely monopolizing mating (15–18). Also problematic are the suggestions that monogamy was a preferred strategy for reducing the risk of infanticide by strange males (19) and that it emerged because male parental care was indispensable to female reproduction. [Data suggest that paternal care had often evolved after monogamy was already established (20).] Recent discussions, instead, focus on communal breeding (4, 6), mate guarding (6), and food-for-mating transactions (5).

However, an important component is missing from these discussions. Many species would, indeed, be much better off evolutionarily if the effort spent on male competition over mating was redirected to increasing female fertility or survivorship of offspring. However, the fact that there is a higher fitness solution to a particular social (or evolutionary) situation does not imply that this solution will be realized. Realizing such a solution may require crossing fitness valleys and/or finding a way to make it stable to the invasion of various mutants. In the context of the transition to pair-bonding, it has been argued that males are locked in a "social dilemma," where shifting one's effort from "appropriation" (i.e., contending with other males for mating success) to "production" (i.e., caring and provisioning) would give an advantage to free-riding competitors and therefore, should not happen (10, 21, 22). In fact, a major challenge for the evolutionary theory is to explain the emergence of group-beneficial behaviors and traits that would be resistant to the invasion of cheaters and free riders (23–25).

Here, I first use simple mathematical models to illustrate the power of the social dilemma faced by males, which results in selective forces strongly opposing the shift from appropriation to production. Then, I propose a general scenario extending and making more specific some of the earlier ideas on how to resolve this dilemma.

Results

I consider a population in which individuals interact in groups comprised of N males and N females. Each male divides his effort between two activities potentially increasing his fitness. One activity is contending for status and dominance with other males in the group. The other activity is directed to females and offspring (e.g., caring for offspring and provisioning or guarding females). I posit that the share S_i of paternity won by male i in direct competition with other males is given by the standard Tullock contest success function of (Eq. **1**)

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$$S_i = \frac{m_i^{\beta}}{\sum\limits_j m_j^{\beta}} \quad [1]$$

which is extensively used in economics (22) and evolutionary biology (10, 13, 26, 27). Here, $0 \le m_i \le 1$ is the fighting effort of male i, and parameter $\beta > 0$ measures the decisiveness of the differences in male fighting effort in controlling the outcome of the competition. Describing the situations where only a few males get most of the matings (which happens in chimpanzees and other species living in hierarchically organized groups) (28, 29) (*SI Appendix*) requires one to assume that β is sufficiently larger than one (e.g., two to four). Using the information in ref. 10, I assume that female fertility is defined by the function (Eq. **2**)

$$B(y) = (C + y)^{\alpha}, \quad [2]$$

where $0 \le y \le 1$ is a male's effort to caring or provisioning and $\alpha > 0$ measures the efficiency of males' effort. Parameter C can be interpreted as a female's contribution to her fertility, and it is set to one. If $\alpha < 1$, the males' effort is less efficient than the effort of females; if $\alpha > 1$, there is a synergy between female and male efforts (i.e., the total effect is greater than the sum of the two). It is reasonable to assume that α does not exceed one by too much (10) (*SI Appendix*).

In the communal care model (10), each male allocates a fraction c_i of his effort to caring for offspring ($c_i + m_i = 1$). The male care is distributed randomly among all offspring in the group and increases female fertility by a factor $B(\bar{c})$, where $\bar{c}$ is the average care in the group. In a group with N females, male i wins a share S_i of paternity in competition with other males, and his fitness is $B(\bar{c})S_iN$.

In the mate-guarding model, male i devotes effort g_i to guarding a particular female ($g_i + m_i = 1$). Guarding effort g_i gives a paternity γg_i of the guarded female's offspring, where $0 \le \gamma \le 1$ is the guarding efficiency. The total unguarded paternity is $\sum(1-\gamma g_i) = N(1-\gamma\bar{g})$, where $\bar{g}$ is the average guarding effort. Male i wins share S_i of this paternity in competition, and his fitness is defined in the second row of Table 1.

In the food-for-mating model, each male allocates effort p_i to provisioning randomly chosen females ($p_i + m_i = 1$). Provisioning at level p_i buys paternity in the amount γp_i, where $0 \le \gamma \le 1$ is the efficiency of provisioning to paternity conversion. Provisioning also increases female fertility by a factor $B(\bar{p})$, where $\bar{p}$ is the average provisioning effort in the group. The total paternity assigned in competition is $B(\bar{p})N(1-\gamma\bar{p})$. The male's fitness is defined in the third row of Table 1, where the first term in the brackets gives paternity bought with food, whereas the second term is paternity won in competition.

The mate-provisioning model is similar to the food-for-mating model, except that each male can provision only one female and each female can be provisioned by only one male. As a result of provisioning, the female's fertility is increased by a factor $B(p_i)$. The total paternity assigned in competition is $\sum_j B(p_j)(1-\gamma p_j)$. The male's fitness is defined in the fourth row of Table 1, where the first and second terms in the brackets give paternity of the provisioned female offspring and paternity won in competition, respectively.

These models can be analyzed using a standard invasion analysis (30–32). A common feature of the four models is that, under the biologically most relevant conditions (i.e., small α, relatively large $\beta \sim 2$–4, and large $N \sim 10$) (33, 34), they all predict (Table 1) evolution to a state where all male effort is devoted to fighting ($m_i = 1$). An alternative dynamic, which is the only other possibility in the first three models, is the evolution to a state where all males exhibit an intermediate fighting effort and the rest of their effort goes to caring or provisioning. In the mate-provisioning model, there is also a possibility that the system evolves to a polymorphic state at which a minority of males devotes all effort to provisioning, whereas remaining males devote all their effort to fighting. Such a polymorphic state is analogous to the states observed in producer–scrounger models (35–38); in the present context, "scroungers" are males who do not invest in females but rather, "steal" paternity. However, all these alternatives require α to be large and/or β and N to be small, which seems to be unrealistic under the conditions inferred for hominins. [For example, with $\beta = 3$ and $N = 10$, α would have to be >27 in the communal care model and >18 in the food-for-mating and mate-provisioning models, where in the latter case, I optimistically assumed $\gamma = 1$. With such large α-values, the effect of males on female fertility, defined in the model as $(1 + p)^{\alpha}$, would have to be enormously large.]

The results summarized in Table 1 assume that groups are formed randomly, which implies low probability of genetic relatedness between individuals. In chimpanzees and likely, hominins, within-group genetic relatedness can be somewhat elevated, because only one sex (females) disperses (39–41). The kin selection theory (23, 25, 42) predicts reduced competition in kin groups. Elevated relatedness does, indeed, reduce between-male competition in the communal care, food-for-mating, and mate-provisioning models. (In the mate-guarding model, relatedness has no effect.) However, in realistic situations, the conditions given in Table 1 will not change substantially (*SI Appendix*).

At the state with $m = 1$, female fertility [$B(0) = 1$] is significantly smaller than the fertility that could be achieved [$B(1) = 2^{\alpha}$] if all males were to devote all their effort to female provisioning or caring for offspring. Males are forced to invest in appropriation rather than production by the logic of social interactions in a promiscuous group, where investing more in offspring means that there is more paternity for other males to steal (10). Thus, the male's dilemma drives the evolution to a low fitness (payoff) state, which is a feature shared by other social dilemmas (e.g., the Prisoner's dilemma or the public goods dilemma) (23–25).

These results have implications for some recent theories of human origins. In particular, the works in refs. 4, 6, and 8 argue for the importance of communal breeding during the origin of humans. Ref. 6 also argues for the importance of mate guarding

Table 1. Summary of models

Model	Variables	Male fitness	Evolution to $m_i = 1$ if
Communal care (10)	m_i, c_i	$w_i = B(\bar{c})S_iN$	$\alpha < \beta(N - 1)$
Mate guarding	m_i, g_i	$w_i = B(0)[\gamma g_i + S_iN(1-\gamma\bar{g})]$	$\gamma < \beta$
Food for mating	m_i, p_i	$w_i = B(\bar{p})[\gamma p_i + S_iN(1-\gamma\bar{p})]$	$\alpha < (\beta - \gamma)(N - 1)$
Mate provisioning	m_i, p_i	$w_i = B(p_i)\gamma p_i + S_i\sum_j B(p_j)(1-\gamma p_j)$	$\alpha < (\beta - \gamma)(N - 1)$
Pair bonding	m_i, p_i	$w_i = \mathcal{B}_i\mathcal{P}_i + S_i^*\sum_j \mathcal{B}_i(1-\mathcal{P}_j)$ $\mathcal{B}_i = B(p_i)C_i, C_i = 1-\varepsilon\mathcal{P}_i^4, \mathcal{P}_i = 1-(1-f_i)(1-\gamma p_i)$	*SI Appendix*

as a preferable strategy after the inequality in strengths between males was reduced by the invention of weapons. My modeling results contradict these arguments. Although switching to communal breeding and mate guarding could increase fitness, it does not happen, because selection is not able to overcome the accompanying free-rider problem.

In contrast, the scenarios, including mate provisioning (5), seem promising because of the "double benefit" of provisioning to males. Indeed, a provisioning male not only gets mating (43), but provisioning also increases fertility of his mate and thus, the number of the male's offspring. However, some additional factors need to be taken in consideration. Here, I focus on two factors that, arguably, are rather general.

The first factor is inequality between males in their fighting abilities, which is always present (28, 29) because of various genetic, developmental, and environmental factors. With strong inequality in strengths, weaker males do not have as much chance of winning between-male competition, and thus, they may be eager to use alternative reproductive strategies (36, 44, 45). In the model, I will assume that each male is characterized by a constant strength s_i drawn randomly from a uniform distribution on interval $(1 \mp \sigma)/2$, where parameter $0 \leq \sigma \leq 1$ measures the extent of the variation in male strengths.

As in the mate-provisioning model, let males divide their effort between provisioning a female and contending with other males for mating with multiple females. I will assume that the male fighting effort is conditioned on his dominance rank in the group. This assumption requires one to model a male strategy not as a scalar as above but as a vector $(m_{i,1}, m_{i,2}, \ldots, m_{i,N})$, where $m_{i,j}$ is the fighting effort of a male with genotype i when at rank j. With nonequal males, I postulate that the share of paternity won by male i is given by Tullock function with m_i substituted by $s_i m_i^*$, where m_i^* is a rank-dependent fighting effort of male i (Eq. **3**):

$$S_i^* = \frac{\left(s_i m_i^*\right)^\beta}{\sum_j \left(s_j m_j^*\right)^\beta}. \qquad [3]$$

The second set of factors is related to the role of females. In the models described so far, females played a passive role. However, because they receive direct benefits from provisioning males, females should be choosy, and they may become, to some extent, faithful to them. [This argument implies that females exert some control over their mating behavior. This assumption is reasonable, because the strongest male(s) can never be in complete control of female mating behavior if there are multiple adult males in the group.] To model these effects, I allow females to differ with respect to their faithfulness. I postulate that the share of paternity obtained by a male with provisioning trait p_i from a female with faithfulness f_i $(0 \leq f_i \leq 1)$ is (Eq. **4**)

$$\mathcal{P}_i = 1 - (1 - f_i)(1 - \gamma p_i). \qquad [4]$$

If $f_i = 0$, then $\mathcal{P}_i = \gamma p_i$ as in the mate-provisioning model. Female faithfulness, if present, is expected to make switching to pair-bonding easier. Indeed, in the mate-provisioning model, if all females have identical faithfulness f, the right-hand side of the inequality in Table 1 must be multiplied by factor $\frac{1-f}{1+f(N-1)}$. High faithfulness f, thus, can significantly weaken the conditions for escaping the $m = 1$ state.

However, polyandry can have multiple genetic and material benefits (including access to better genes, increasing the probability of fertilization, preventing infanticide, receiving support from males in agonistic interactions, etc.) (46–48), and therefore, switching to monogamy can result in fitness costs. Therefore, I conservatively posit that female fertility declines with the paternity $\mathcal{P}_i$ obtained by her pair mate. Specifically, I assume that fertility is reduced by a factor (Eq. **5**)

$$C_i = 1 - \varepsilon \mathcal{P}_i^4, \qquad [5]$$

where ε is the maximum reduction of fertility (observed when monogamy is strict; i.e., $\mathcal{P}_i = 1$). This quartic function captures a reasonable assumption that fertility costs of pair-bonding become significant only when paternity $\mathcal{P}_i$ obtained by the partner is sufficiently large.

Females have an incentive to bond with provisioning males. Simultaneously, provisioning males have an incentive to bond with females who remain faithful to them; the more the male's effort to provisioning, the stronger the incentive. These factors are expected to lead to nonrandom pair formation. To describe it, I use a simple model in which the probability of a mating bond between male i and female j is proportional to (Eq. **6**)

$$\psi_{ij} = \exp(\omega f_i p_j). \qquad [6]$$

Parameter ω scales the range of possible ψ values: the minimum is one (at $p = 0$ or $f = 0$), and the maximum is $\exp(\omega)$ (at $p = f = 1$). In the terminology of nonrandom mating models (49, 50), Eq. 6 describes open-ended preference.

As shown above, with high female faithfulness, males are expected to switch to provisioning. Will female faithfulness increase if starting with low values? To get intuition, we can evaluate evolutionary forces acting on female faithfulness. Assuming that the average value of p as well as the variances of f and p are small, the invasion analysis shows (see *SI Appendix*) that faithfulness f will increase when small if $4\gamma^3 p^2 \varepsilon < \omega$ (that is, if the benefit of promiscuity, ε, is not too large, and the assortativeness in pair formation, ω, is strong enough). Increasing female faithfulness f should cause the evolution of increased male provisioning p. As male provisioning trait p increases, female faithfulness f will evolve to higher and higher values until it stabilizes at a level controlled by a balance between selection for good genes and access to food provisioned by males.

This argument is based on the consideration of separate components of the pair-bonding model. To check this logic, I have performed stochastic individual-based simulations. I considered a finite population of sexual diploid individuals subdivided into G groups. The results confirm the expectation (*SI Appendix*). When the fitness benefit of promiscuity (ε) is large enough and/or the variation in male strengths (σ) is low, the population evolves to a low fitness state with $m = 1$ and no female provisioning (Fig. 1 *A* and *C*). When both the fitness benefit of promiscuity is not too large and the variation in male strengths is significant, the population exhibits a strikingly different dynamics shifting to a high fitness pair-bonding state with high levels of male provisioning and female faithfulness (Fig. 1 *B* and *D*). At the end, except for a very small proportion of the top-ranked individuals, males invest exclusively in provisioning females who have evolved very high fidelity to their mates. The shift to pair-bonding occurs in a sequence of transitions in the strategies of males of different rank, starting from the lowest rank and going up to the highest ranks. Occasionally the model exhibits cycling behavior when both female faithfulness f and male provisioning traits p for the top-ranked males fluctuate (*SI Appendix*). The cycling occurs because once most males are provisioning, female faithfulness is not selected for anymore. Then selection against monogamy takes over with females evolving decreasing faithfulness, which in turn forces top-ranked males to reduce their provisioning and increase their investment in competition.

Discussion

The transition from promiscuity to pair-bonding in a species living in hierarchically organized groups requires a mechanism

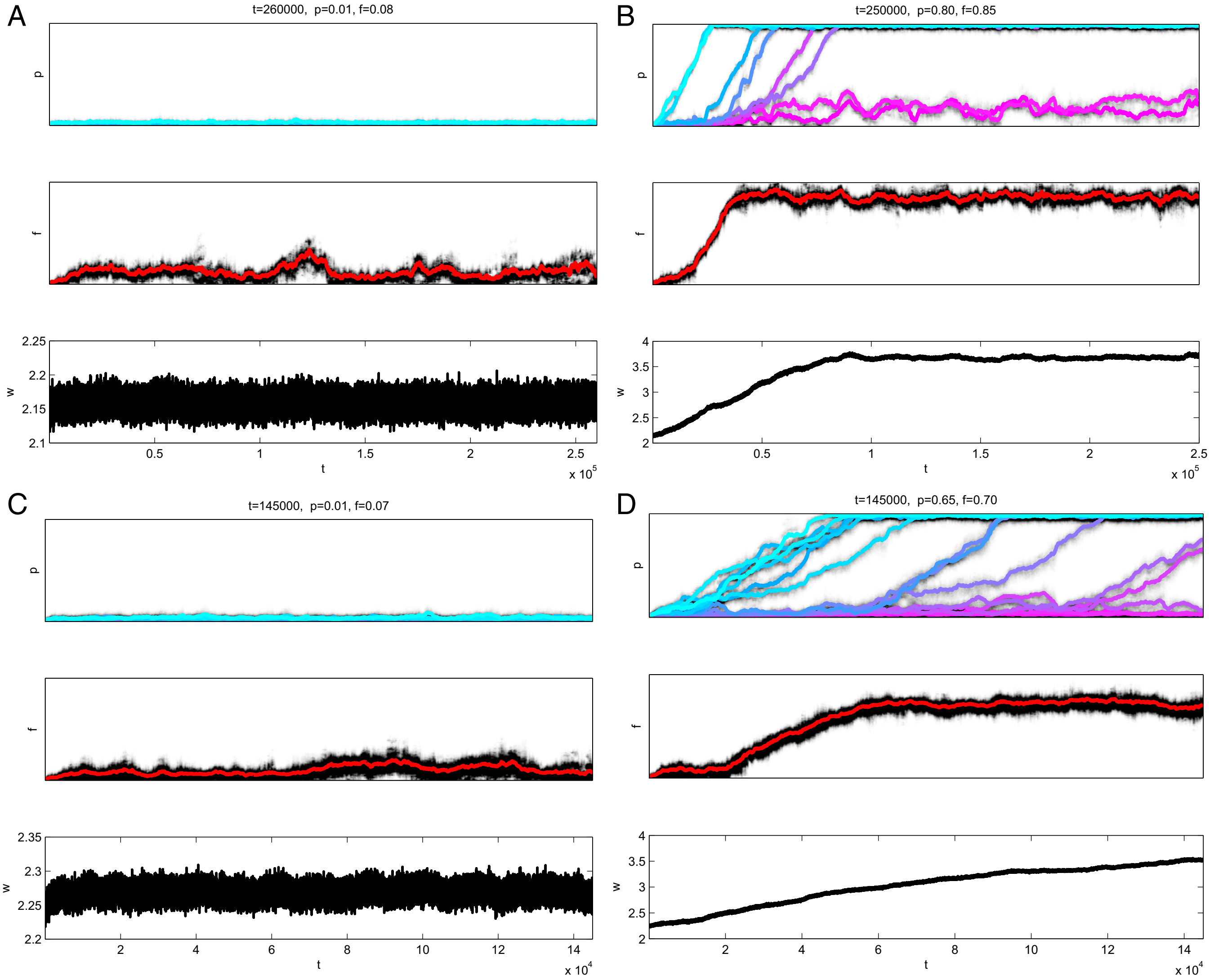

Fig. 1. Examples of long-term evolutionary dynamics. (*A* and *C*) Small variation among males ($\sigma = 0.25$). (*B* and *D*) Large variation among males ($\sigma = 1$). (*A* and *B*) $N = 8$, $\varepsilon = 0.05$. (*C* and *D*) $N = 16$, $\varepsilon = 0.1$. Other parameters: $\alpha = 1$, $\beta = 3$, $\gamma = 0.5$, $\omega = 1$. In *A*–*D*, *Top* shows male provisioning traits p_i for males of different rank from low (cyan) to high (magenta), *Middle* shows female faithfulness trait f, and *Bottom* shows the average fitness. The colored curves showing mean trait values are superimposed on the graphs to show the distributions of the traits using the gray color scheme. The numbers on top of sets of graphs show the final generation and the average values of p and f at this generation.

that would resolve the male's dilemma, i.e., the conflict between investing in appropriation and production, in favor of the latter (10). Several such mechanisms have been recently advanced in the literature, including those focusing on communal care, mate guarding, and mate provisioning (4–8). Using a series of simple models that build on earlier work (10), I have shown that, under biologically realistic conditions (e.g., when the group size is not too small, competition between males is strong, and the effects of male provisioning and care are not too large), the population is not able to escape the low fitness state at which males invest exclusively into competition for mating. This conclusion is not changed qualitatively, even if one accounts for an elevated genetic relatedness between males arising from their philopatry. Note that communal care provided by females, the importance of which has been stressed in a number of recent publications (4, 6–8), is even less likely to become established because of low relatedness between females who disperse to different groups on maturity. Moreover, females may benefit from multiple matings (46–48), which implies additional selection against pair-bonding. The power and implications of the male's dilemma discussed above have not been generally acknowledged in the discussions of human transition to pair-bonding (10).

The solution of the male's dilemma proposed here builds on the idea of mate provisioning augmented by the explicit consideration of (*i*) females' evolutionary response to provisioning and (*ii*) the role of males' dominance ranks in determining their preferred actions. Mate provisioning has double benefits, one of which (mating) is immediate and another (increased fertility and decreased between-birth interval) is delayed. These benefits are most pronounced for low-ranked males who have a low chance of winning a mate in competition with top-ranked males. One, therefore, should expect that it is low-ranked males who will attempt to buy mating by provisioning. Note that, if there are more males at the bottom than at the top of the hierarchy, selection benefiting the "masses" may become stronger than selection benefiting the "elite". Top-ranked males can easily beat out or chase away the low-ranked males and steal the paternity, making the investment of low-ranked males in production wasteful.

However, after females start developing preferences for being provisioned, the low-ranked males' investments start to pay off. In the model presented here, male provisioning and female faithfulness coevolve in a self-reinforcing manner. At the end, except for a very small proportion of the top-ranked individuals, males invest exclusively in provisioning females who have evolved very high fidelity to their mates. Overall, females are not predicted to become completely faithful, but rather, the level of their faithfulness is expected to be controlled by a balance between selection for better genes (potentially supplied by top-ranked males) and better access for food and care (provided largely by low-ranked males).

Overall, my results confirm the theoretical plausibility of what has been viewed as a critical step in the evolution of our own species—the transition from promiscuity to strong pair-bonding. The model shows that such a sexual revolution could have been initiated by low-ranked males who started provisioning females to get matings; after the process got underway, it would lead to a kind of self-domestication, and the end result is a group-living species comprised of provisioning males and largely faithful females.

The results highlight the importance of considering the joint evolutionary dynamics of male and female traits. The model shows that nonrandom pair formation can have dramatic effects on evolutionary dynamics. The results emphasize the need for incorporating between-individual variation in theoretical and empirical studies of social dilemmas and behaviors; the commonly used simplifying assumption that individuals are identical can significantly bias the conclusions.

The models introduced and analyzed here assume that, initially, both sexes mate promiscuously. It is important to realize, however, that an underlying reason for the male's dilemma as studied here is female promiscuity and the associated risks that the male's investment in production might be stolen by other males. Therefore, some of my results may be relevant for polyandrous species. In polygynous species, male promiscuity may lead to another dilemma for males: whether to invest in obtaining more females or providing better provisioning and care to a smaller number of females. This other version of the male's dilemma between production and appropriation is outside the scope of this work.

The importance of food-for-sex exchanges (5, 43, 51) in chimpanzees has been recently questioned in ref. 52, which argues that the benefits to females of food provisioned by males are small, whereas the role of female selectivity in determining male reproductive success is limited. Population genetic models tell us, however, that even weak evolutionary forces can result in dramatic phenotypic or behavioral changes if they act over multiple generations. A recent metaanalysis (53) shows correlation between male-to-female food transfer and the opportunity for female mate choice. There are some additional anatomical features of humans—bipedalism, hidden ovulation, and permanently enlarged mammary glands—that are easier to explain in terms of the pair-bonding model than the mate-guarding and communal breeding models (5, 54).

New paleontological data on 4.4-Myr-old fossils of *Ardipithecus ramidis* show that this species already had a reduced sexual size dimorphism and strong reduction in upper canine teeth (5). This finding and a loss of morphological adaptations to sperm competition in humans (5, 55) suggest that strong decline in the intensity of male-to-male conflict, which is one of the consequences of the transition to pair-bonding, happened soon after the hominins/chimpanzees divergence (5). If true, this finding has important implications for the theories of the runaway evolution of human brain size and intelligence over the past couple hundred thousand years. One controversial set of ideas (1, 2, 56–61) coming under the rubric of the "Machiavellian intelligence" or "social brain" hypothesis identifies selective forces resulting from within-group social competitive interactions as the most important factors in the evolution of hominids, who at some point in the past, became an ecologically dominant species (1, 2). These forces selected for more and more effective strategies (including deception, manipulation, alliance formation, exploitation of the expertise of others, etc.) of achieving social success and learning to use them. The social success translated into reproductive success (e.g., more children) (62, 63) selecting for larger and more complex brains. Pair-bonding would significantly decrease the efficiency of selection resulting from within-group competition for mating success. This effect would likely rule out within-group competition as a source of selection for larger brain size and intelligence. An intriguing alternative is selection resulting from between-group competitive and cooperative interactions.

The transition to strong pair-bonding opened a path to intensified male parental investment, which was a breakthrough adaptation with multiple anatomical, behavioral, and physiological consequences for early hominids and all of their descendants (4–6). The establishment of pair-bonding shifted competition between males for mates, which was potentially destructive for the group, to a new dimension which is beneficial for the group — competition to be a better provider to get better mates (64). Pair-bonding provided a foundation for the later emergence of the institution of modern family (65) as an outcome of additional processes, such as wealth accumulation and inheritance (66). Pair-bonding also made possible the recognition of male kin, dramatically expanding the efficiency of kin selection and helping by grandparents, leading to stronger within-group coalitions and alliances (67, 68), and allowing for subsequent evolution of widespread cooperation in general (6, 69).

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Supplementary Information for S.Gavrilets "Human origins and the transition from promiscuity to pair-bonding"

Contents

Effects of α and β

Figure S1 shows the effects of parameter α on female fertility $B(p)$. Figure S2 shows the expected mating success $E\{S\}$ for males of different ranks assuming maximum mating effort (i.e. all $m_i = 1$) with $N = 8$ and different values of σ and β. These graphs were obtained by generating individuals strengths $s_1, \ldots, s_8$ by random independent sampling from a uniform distribution on $1/2 \mp \sigma/2$ and then evaluating mating success as predicted by the Tullock function

$$S_i = \frac{s_i^\beta}{\sum_j s_j^\beta}. \tag{1}$$

To produce the graphs, I used 500 randomly generated sets of data for each parameter combination. Empirical rank-mating success curves for primates typically show strong inequality in reproductive success with most of the mating going to a couple of the top-ranked males(1, 2, 3, 4). This suggests that both β and σ should be at the upper half of values considered here.

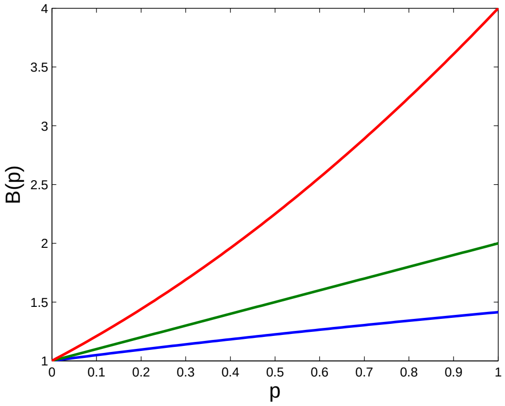
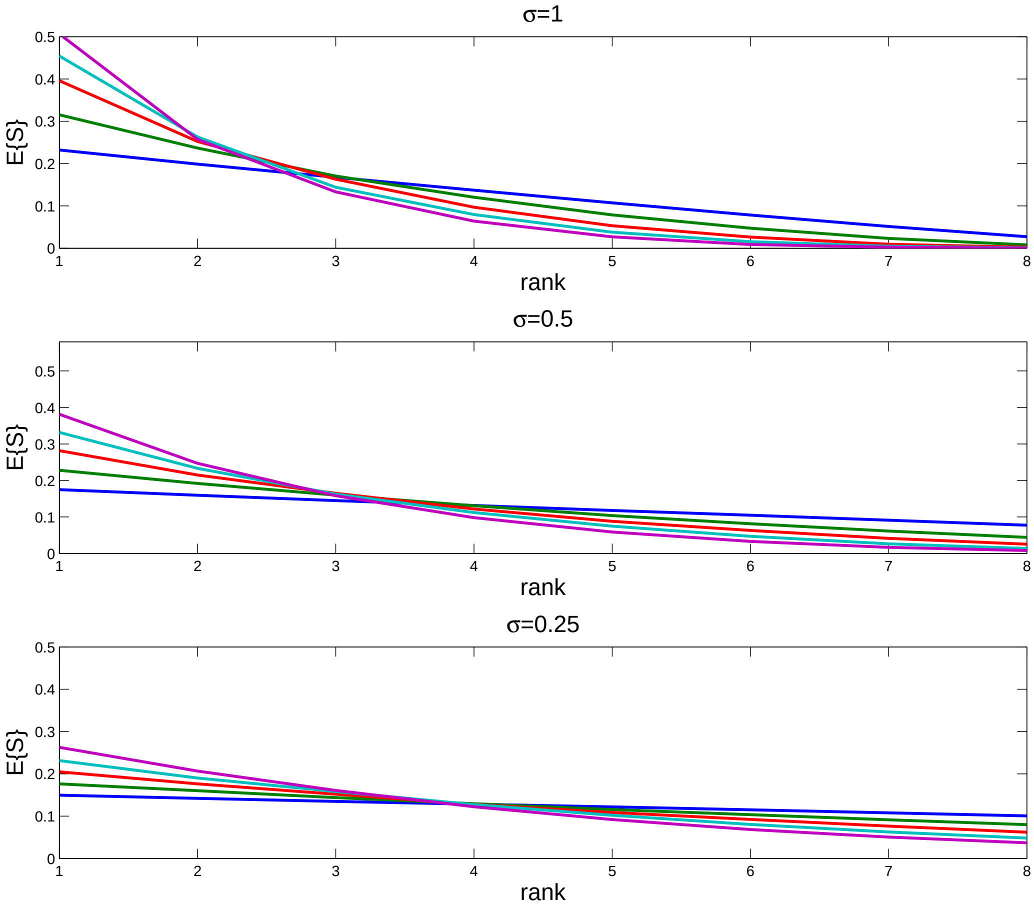


Figure S1: Female fertility $B(p) = (1 + p)^\alpha$ as a function of male provisioning effort p for $\alpha = 0.5, 1$ and 2 (bottom to top).



(a)

Figure S2: Expected mating success $E\{S\}$ for males of different ranks with $N = 8$, three different values of σ (shown on the graphs), and five different values of β ($1, 2, 3, 4, 5$, identified by lines of different colors; bottom to top).

Communal breeding

I start by describing a model introduced by Ref.(5) and then generalizing it for the case of relatedness. Each male divides his effort between caring for offspring (c) and contending with other males for mating opportunities (m) ($c + m = 1$). Male care is distributed randomly among all offspring in the group. In a group of N male and N females, male i fitness is defined as

$$w_i = B(\bar{c})S_iN, \tag{2}$$

where $\bar{c}$ is the average care received by offspring of a female. Using the invasion analysis, let c and m be the corresponding efforts of $N - 1$ resident males and $\tilde{c}$ and $\tilde{m}$ be that of a single mutant male. The invasion fitness is

$$w(\tilde{c}|c) = B\left(\frac{\tilde{c}+(N-1)c}{N}\right)\frac{\tilde{m}^\beta}{\tilde{m}^\beta+(N-1)m^\beta}N.$$

Making substitutions $m = 1-c$ and $\tilde{m} = 1-\tilde{c}$ and evaluating the derivative $\frac{dw}{d\tilde{c}}$ at $\tilde{c} = c$, we find that the invasion fitness gradient is

$$\frac{dw}{dc} = \frac{(1+c)^{\alpha-1}}{N(1-c)}\left[-(\alpha+\beta(N-1))c-\beta(N-1)+\alpha\right]$$

If

$$\beta(N-1) > \alpha, \tag{3a}$$

then the expression in the brackets is always negative and c is predicted to evolve to 0. Otherwise, c evolves to an intermediate value

$$c^* = 1-\frac{2\beta(N-1)}{\beta(N-1)+\alpha}. \tag{3b}$$

Computing the second derivative of the invasion fitness at $c = c^*$, we find that

$$\frac{d^2w}{d\tilde{c}^2}|_{\tilde{c}=c} = -\frac{1}{4}\left(\frac{2\alpha}{\alpha+\beta(N-1)}\right)^\alpha\frac{(\alpha+\beta(N-1))^2}{\alpha\beta N^2(N-1)}\left[\beta(N-1)+\alpha(N+\beta)\right]$$

which is always negative. Therefore, the equilibrium c^* is evolutionarily stable.

Relatedness. The above analysis can be extended to the case when males in the group are related. Specifically I assume that on average there is not one but k mutants in a group and write k as $k = 1+r(N-1)$. Here r is the probability that a random group-mate of a mutant is also mutant. Within the framework of our invasion analysis when mutants are rare, r is the average relatedness coefficient in the group (6). In general, r will depend on some model details which however is irrelevant for our derivations. What is necessary though is that r remains approximately constant during evolutionary dynamics. With equal individuals contributing equally on average to the next generation offspring and with small changes in c and m per generation, the assumption of approximate constancy of r is justified. Then the invasion fitness becomes

$$w(\tilde{c}|c) = B\left(\frac{k\tilde{c}+(N-k)c}{N}\right)\frac{\tilde{m}^\beta}{k\tilde{m}^\beta+(N-k)m^\beta}N.$$

while the equations (3a) and (3b) become

$$\beta(N-1)\,\frac{1-r}{1+r(N-1)} > \alpha,$$
$$c^* = 1-\frac{2\beta(N-1)(1-r)}{\beta(N-1)(1-r)+\alpha[1+r(N-1)]},$$

respectively. These equations have a bit more compact form if one uses k instead of r.

Mate guarding

In this model, each male divides his effort between guarding a particular female (g) and contending with other males for mating opportunities (m) ($g + m = 1$). Assume first that guarding is 100% efficient. Male i fitness is

$$w_i = g_i + S_i \sum_j (1 - g_j), \tag{4}$$

where the sum describes the total share of paternity open for competition. Using the same notation as above, the invasion fitness can be written as

$$w(\tilde{g}|g) = \tilde{g} + \frac{\tilde{m}^\beta}{\tilde{m}^\beta + (N-1)m^\beta} \left[1 - \tilde{g} + (N-1)(1-g)\right],$$

where $m = 1 - g, \tilde{m} = 1 - \tilde{g}$. The invasion fitness gradient is

$$\frac{dw}{dg} = \frac{N-1}{N}(1-\beta),$$

so that g evolves to 0 if

$$\beta > 1, \tag{5a}$$

and to 1 otherwise.

Imperfect guarding. If guarding efficiency is not perfect, so that

$$w_i = \gamma g_i + S_i \sum_j (1 - \gamma g_j),$$

where $\gamma < 1$ is the efficiency of guarding, then the invasion fitness gradient is

$$\frac{dw}{dg} = \frac{N-1}{N} \, \frac{\gamma - \beta - \gamma g(1-\beta)}{1-g}.$$

From this, one concludes that g evolves to 0 if

$$\beta > \gamma. \tag{5b}$$

and to

$$g^* = \frac{\gamma - \beta}{\gamma(1-\beta)} \leq 1$$

otherwise.

Computing the second derivative of the invasion fitness at g^* we find that

$$\frac{d^2 w}{d\tilde{g}^2}|_{\tilde{g}=g} = -\frac{(1-\beta)^2\gamma^2(N-1)}{\beta(1-\gamma)N}$$

which is always negative. Therefore, the equilibrium g^* is evolutionarily stable.

Relatedness. The above result is not qualitatively affected by the relatedness of males. The only difference is that the first factor in the right-hand side of the equation for $\frac{dw}{dg}$ becomes $(N-k)/N$ so that the rate of evolution is decreased.

Food-for-mating

In this model, each male divides his effort between provisioning females (p) and contending with other males (m) for mating opportunities, ($p+m=1$). Provisioning at level p buys paternity in the amount γp ($0 \leq \gamma \leq 1$). Provisioning is distributed among females randomly. Provisioning increases female fertility by a factor $B(\overline{p})$. Male i fitness is

$$w_i = B(\overline{p})[\gamma p_i + S_i(1-\gamma\overline{p})N]. \tag{6}$$

The first term in the brackets gives paternity bought with food while the second term is paternity won in competition. Note that if $\gamma = 0$ (so that provisioning does not buy any paternity), the model becomes equivalent to the communal breeding model. If $\alpha = 0$, so that $B(\overline{p}) = 1$, the model becomes equivalent to the mate guarding model.

In this model the invasion fitness gradient is $\frac{dw}{dp} = \frac{B(p)}{N(1-p^2)}H(p)$, where quadratic

$$H(p) = \gamma(\beta-1)(N-1)p^2 - [\alpha + \beta(1-\gamma)(N-1)]p + \alpha - (\beta-\gamma)(N-1),$$

Note that $H(0) = \alpha - (\beta-\gamma)(N-1), H(1) = -2\beta(1-\gamma)(N-1) < 0$ and $H(0)' = -\alpha - \beta(1-\gamma)(N-1) < 0$. We observe that

- If $\beta > 1$ and $\alpha < (\beta-\gamma)(N-1)$, then $H(p) < 0$ for all p and $p \to 0$.
- If $\alpha > (\beta-\gamma)(N-1)$, then $H(0) > 0, H(1) < 0$ and p evolves to an intermediate value.
- If $\beta < 1$ and $\alpha < (\beta-\gamma)(N-1)$, then both $H(0)$ and $H(1)$ are negative. Also negative is $H(0)'$ so that no other roots are present and $H(p) < 0$. Therefore $p \to 0$.

Summarizing, if

$$\alpha < (\beta-\gamma)(N-1),$$

then $p \to 0$. Otherwise p evolves to an intermediate value p^* given by a positive root of quadratic equation $H(p) = 0$. Assuming $\gamma = 0$ or $\alpha = 0$ simplifies the above conditions to those in the communal breeding model and in the mate guarding model, respectively, as it is supposed to.

The second derivative of the invasion fitness $\frac{d^2w}{d\tilde{p}^2}|_{\tilde{p}=p}$ can be found in a straightforward way but the resulting equation is rather messy. Numerical analysis however suggests that at p^* this derivative is always negative so that this equilibrium is evolutionarily stable.

There are some similarities between the behavior of this model and that in (7). (7) studied the male's dilemma regarding splitting his effort between the investments into sperm competition and into female fecundity stimulation. In their model, there are no more than 2 males ($N = 2$) and coefficient β was set to 1. According to our results, these are parameter values greatly simplifying the shift towards production. Although the models differ in many details, (7) did observe that sufficiently large α causes the males to invest exclusively in female fecundity stimulation.

Relatedness. With relatedness, the equation for H becomes

$$H(p) = \gamma(\beta - 1)(N - k)p^2 - [\alpha k + \beta(1 - \gamma)(N - k)]p + \alpha k - (\beta - \gamma)(N - k),$$

where $k = r(N - 1)$ is the number of other mutants in the group and r is relatedness. Then $p \to 0$ if

$$\alpha < \frac{(1 - r)}{1 + r(N - 1)}(\beta - \gamma)(N - 1),$$

and to an intermediate value otherwise.

Mate provisioning

Each male divides his effort between provisioning a particular female (p) and contending with other males for mating opportunities (m) ($p + m = 1$). Provisioning effort p buys γp units of paternity ($\gamma < 1$) of that female offspring and simultaneously increases her fertility by factor $B(p)$. Male i fitness is

$$w_i = B(p_i)\gamma p_i + S_i \sum_j B(p_j)(1 - \gamma p_j), \tag{7}$$

The invasion fitness is

$$w(\tilde{p}|p) = B(\tilde{p})\gamma\tilde{p} + \frac{\tilde{m}^\beta}{\tilde{m}^\beta + (N - 1)m^\beta}\left[B(\tilde{p})(1 - \gamma\tilde{p}) + (N - 1)B(p)(1 - \gamma p)\right]$$

which leads to an invasion fitness gradient in the form of $D_p = \frac{(1+p)^\alpha}{N(1-p^2)}H(p)$, where quadratic

$$H(p) = \gamma(\beta - 1 - \alpha)(N - 1)p^2 - [\alpha + \beta(1 - \gamma)(N - 1) - \alpha\gamma(N - 1)]p + \alpha - (\beta - \gamma)(N - 1),$$

Note that $H(0)$ and that $H(1)$ are the same as in the previous model. However $H'(0)$ is now $-\alpha - \beta(1-\gamma)(N-1) + \alpha\gamma(N-1)$ and can be positive. Note that p can increase from very small values only if $\alpha > (\beta-\gamma)(N-1)$ and that increasing the group size N makes it more difficult.

Assume that $\beta - \alpha - 1 > 0$. If $H(0) < 0$, then $H < 0$ for all p, and the system evolves to the state with $p = 0$ (i.e. $m = 1$). If $H(0) > 0$, then p evolves to an intermediate value p^* given by solution $H(p^*) = 0$. Let $\beta - \alpha - 1 < 0$. Then if $H(0) > 0$, p evolves to an intermediate value p^*. If $H(0) < 0$, than equation

$H(p) = 0$ has zero or two roots between 0 and 1. In the former case, $p \to 0$ always. In the later case, for small initial p, p evolves to 0 while for larger initial values p evolves to p^* which is the largest root. The threshold separating these two regimes is given by the smallest root of $H(p)$. A numerical study shows that the second regime occurs in a very narrow range of parameters.

Summarising, if

$$\alpha > (\beta - \gamma)(N - 1), \tag{8}$$

when p evolves to an intermediate value p^*. If the above condition is not satisfied, then p typically evolves to zero except that if $\beta < \alpha + 1$, there is a small range of parameter values when the system can be bistable. That is, for small initial value of p it evolves to 0 while for large enough initial values p evolves to an intermediate value. A sufficient (but not necessary) condition for evolution to $p = 0$ is this case is $H'(0) < 0$ which takes form

$$\beta > \alpha \ \frac{\gamma(N-1) - 1}{(1-\gamma)(N-1)}.$$

With large N, this simplifies to $\beta > \alpha\gamma/(1 - \gamma)$.

Relatedness. If there is not one but k mutants per group, $H(0)$ is increased by $(\alpha + \beta - \gamma)k$ which increases the plausibility of evolving to an intermediate value of m.

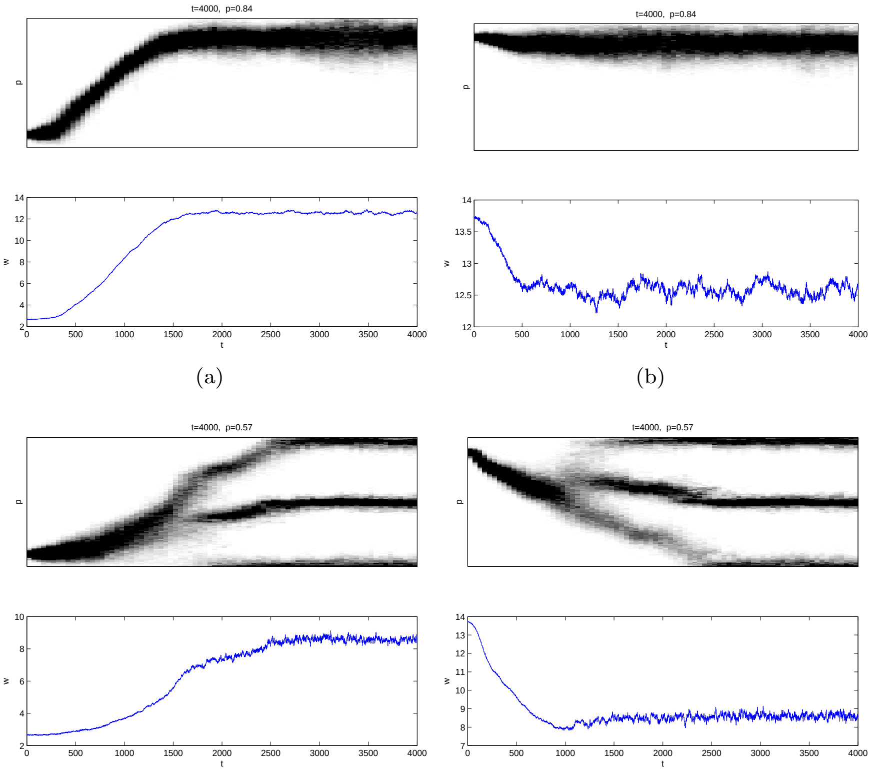
Branching point and mixed strategy. Whether an intermediate equilibrium p^* is evolutionarily stable depends on the sign of the second derivative of the invasion function $\frac{d^2w}{d\tilde{p}^2}|_{\tilde{p}=p}$. Although an algebraic expression for this derivative can be found in a straightforward way, it is rather messy. Numerical analysis of $\frac{d^2w}{d\tilde{p}^2}|_{\tilde{p}=p}$ suggests however that depending on parameters, the equilibrium can be either stable or not. In the latter case, p^* is a branching point so that the distribution of male allele effects become dimorphic (8, 9). Numerical individual-based simulations show that in this case the system evolves to a state at which a minority of males invests exclusively in provisioning whereas the remaining males invest exclusively in mating effort. The latter males can be viewed as scroungers stealing paternity. Figure S3 illustrates the dynamics just described.

One can approximate the frequencies of males of both types. We say that a male plays strategy p if p is his efforts towards provisioning a female. Consider a resident population in which a proportion ϱ of males plays strategy 0 whereas the remaining part $1 - \varrho$ plays strategy 1. Assume there is a small frequency of mutants playing 0 and 1 with probabilities $\tilde{\varrho}$ and $1 - \tilde{\varrho}$, respectively. Consider fitness of a mutant in a group of size N which has n residents playing strategy 0. If the mutant plays 0, his fitness is

$$U_n = \frac{1}{n+1}\left[(N - n - 1)B(1) + (n + 1)B(0)\right],$$

where $B(0) = 1$ and $B(1) = 2^{\alpha}$. If the mutant plays 1, his fitness is $V_n = B(1)$. Let

$$Q_n = \left(\begin{array}{c} N-1 \\ n \end{array} \right) \varrho^n (1-\varrho)^{N-n-1}$$



(a) (b)

(c) (d)

Figure S3: Examples of evolutionary dynamics during 4000 generations. (a) and (b): Evolution towards an ESS. Two runs with different initial conditions. Parameters: $N = 8, \alpha = 3, \beta = 1, \gamma = 0.8, \mu = 0.001$. (c) and (d): Evolution towards a branching point with subsequent divergence. Two runs with different initial conditions. Parameters the same as in (a) and (b) except that $\gamma = 0.6$. Shown are the distribution of the provisioning trait using gray scale (top) and the average female fertility (bottom). In the case of branching, the distribution of the allelic effects is bimodal, but the phenotypic distribution (as shown) is trimodal because individuals are diploid.

be the probability that in the group there are n residents playing 0. [This assumes that the groups are formed randomly.] Then the invasion fitness is

$$w(\tilde{\varrho}|\varrho) = \sum_{i=0}^{N-1} Q_n \tilde{\varrho} \frac{(N-n-1)B(1) + (n+1)B(0)}{n+1} + (1-\tilde{\varrho})Q_n B(1).$$

After simplifications, the selection gradient is

$$\frac{\partial w(\tilde{\varrho}|\varrho)}{\partial \tilde{\varrho}}|_{\tilde{\varrho}=\varrho} = \frac{B(1)[1-(1-\varrho)^N] - (2B(1)-1)\varrho}{\varrho}.$$

From here we conclude that the frequency of males paying strategy 0 is approximately

$$\varrho^* \approx \frac{B(1)}{2B(1)-1}$$

which is asymptotically approaching 1/2 from above as $B(1) \to \infty$. Note that the existence of the mixed equilibrium does not depend on β. Presumably, β affects its stability.

A summary on the effects of relatedness

The kin selection theory (10, 11, 12) predicts reduced competition in kin groups. This is indeed what happens in the communal care, food-for-mating and mate provisioning models. Specifically, with average genetic relatedness in the group, r, the right-hand side of the inequalities in Table 1 must be multiplied by factor $\frac{1-r}{1+r(N-1)}$ which is < 1. Relatedness thus weakens the conditions for escaping the state with $m = 1$. (In the mate guarding model, relatedness has no effect.) However with realistically small values of r, the conditions given in Table 1 will not change substantially. (For example, if half of the group offspring disperses randomly while the rest stay in the native group, $r \approx 4/(3N)$ (6).)

Pair-bonding

The pair bonding model has three additional components not yet consider in the models above. These are female faithfulness, cost of monogamy, and assortative pair-bond formation. We consider these components separately.

Female faithfulness. Females can be to some extent faithful to the males that provision them. Let f_i be the faithfulness of the female i. Male fitness w_i above can be rewritten as

$$w_i = B(p_i)\mathcal{P}_i + S_i \sum_j B(p_j)(1 - \mathcal{P}_i), \tag{9}$$

with male paternity of the provisioned female offspring $\mathcal{P}_i = \gamma p_j$. Introducing female faithfulness f we can generalize $\mathcal{P}_i$ to

$$\mathcal{P}(p_i, f_i) = 1 - (1 - f_i)(1 - \gamma p_j).$$

Note that paternity is $\mathcal{P} = 1$ if the female is completely faithful, $f_i = 1$. If $f_i = 0$, we recover $\mathcal{P}_i = \gamma p_j$. For the pair-bonding model, the terms $H(0), H(1)$ and $H'(0)$ above change to

$$\begin{aligned}
H(0) &= [1 + f(N-1)]\alpha - (1-f)(\beta - \gamma)(N-1),\\
H(1) &= -2\beta(1-f)(1-\gamma)(N-1) < 0,\\
H'(0) &= -\alpha[1 + r(N-1) + (1-r)\gamma(N-1)] - (1-r)\beta(1-\gamma)(N-1)
\end{aligned}$$

Now evolution towards intermediate value of p requires

$$\alpha > \frac{1-f}{1+f(N-1)}\,(\beta - \gamma)(N-1), \tag{10}$$

That is increasing female faithfulness f increases the plausibility of an intermediate equilibrium.

Benefit of promiscuity. Under many conditions females benefit from mating with multiple males (13, 14, 15, 16, 17, 18). We can capture this by assuming that female fertility declines as paternity P of her mate increases. This can be described by the following substitution in the model equations

$$B(p_i) \to B(p_i)C_i,$$

where $C_i = 1 - \varepsilon \mathcal{P}_i^k$ captures the cost of monogamy with ε being the maximum decline in fertility and k being a positive parameter. Then the male fitness becomes

$$w_i = \mathcal{B}(p_i)\mathcal{P}_i + S_i \sum_j \mathcal{B}(p_j)(1 - \mathcal{P}_j). \tag{11}$$

where $\mathcal{B}(p_i) = B(p_i)C_i$ is female fertility.

Sexual selection on faithfulness. We write the expected fitness of a female with faithfulness f in a population with some distribution of the male provisioning trait p as

$$w(f) = \mathrm{E}_p \left\{ B(p)C(f,p) \frac{\psi(f,p)}{\mathrm{E}_f\{\psi(f,p)\}} \right\}$$

where the outside expectation is taken over all males, the inside expectation is taken over all females in the group, and the ratio is the probability of $f \times p$ pairing. Assuming that the variation in f and p is small, $w(f)$ can be approximated as

$$w(f) \approx B(\overline{p})[1 - \varepsilon \mathcal{P}(f,\overline{p})^k] \frac{\psi(f,\overline{p})}{\psi(\overline{f},\overline{p})} = B(\overline{p})[1 - \varepsilon \mathcal{P}(f,\overline{p})^k] \exp(\omega(f - \overline{f})\overline{p}),$$

where $\overline{f}$ and $\overline{p}$ are the corresponding mean values. From here and using $\mathcal{P}(f,p) = 1 - (1-f)(1-\gamma p)$, the invasion fitness gradient at $f = 0$ is

$$D_f = B(p) \left[\omega p - (\gamma p)^{k-1}(k + \omega \gamma p^2 - k\gamma p) \right].$$

With $k = 4$ and small p, this is approximately $B(p)p(\omega - 4\varepsilon\gamma^3 p^2)$. Assuming that p is maintained at some low level (e.g. by a mutation-selection-drift balance), $f = 0$ is locally stable if

$$\varepsilon > \frac{\omega}{4\gamma^3 p^2},$$

that is, if the advantage of promiscuity is sufficiently large.

Numerical simulations

In numerical simulations, male- (p) and female-expressed (f) traits were controlled by two unlinked additive autosomal loci with a continuum of alleles produced by mutation. The following is a list of parameter value varied in simulations: $N = 4, 8, 16; \alpha = 0.5, 1.0, 2.0; \beta = 2, 3, 4; \gamma = 0.25, 0.50, 0.75; \sigma = 0.25, 0.50, 1.00; \omega = 0.5, 1.0, 2.0; \varepsilon = 0, 0.05, 0.10$. The mutation rate per gene per generation was 10^{-3}, the effects of mutations were chosen from a uniform distribution on interval $[-0.05, 0.05]$. Given a mutation, p values at all ranks were modified independently. There were $G = 400$ groups. Male offsping stayed in the native group while females dispersed randomly. Selection was hard with the expected number of offspring of a female set to $2(1.02 + \varepsilon)B$. The actual offspring number was determined using a stochastic variance-reduction procedure analogous to that in Ref.(5). I also enforced an equal number of daughters and sons for each female.

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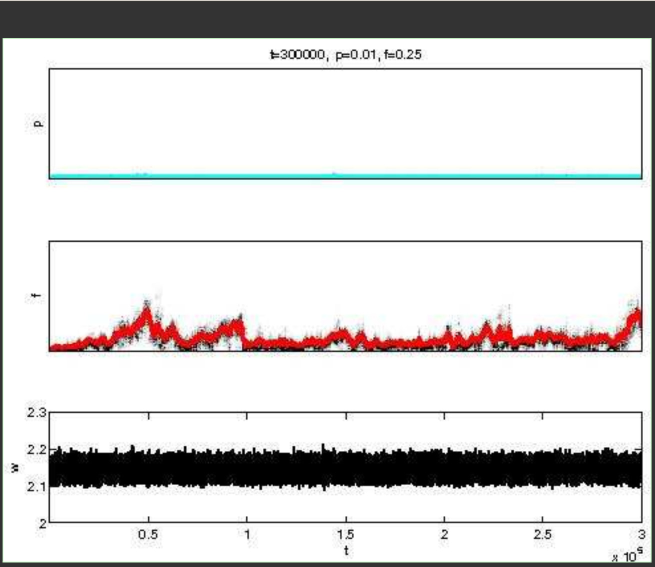
Image gallery

The figures to follow illustrate the dynamics observed in numerical simulations for a sample of parameter combinations. The parameter values are shown under each graph. For example, N4.a0.5b3.0g0.25.o1.00.s0.e0.05.1.eps means that $N = 4, \alpha = 0.5, \beta = 3.0, \gamma = 0.25, \omega = 1.00, \sigma = 0.25$ and $\varepsilon = 0.05$. (The last number 1 should be ignored.) On top of each graph I show the final generation t as well as the average values of p and f traits across the population at the last generation.

Image Gallery
for /home/sergey/share/Mono/Newton/Long_runs/N4/

Number of images: 54
Created on: Friday 01 July 2011



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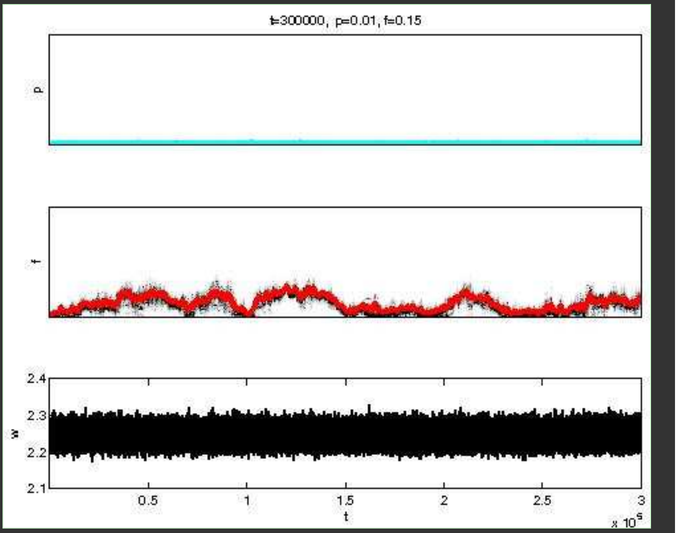

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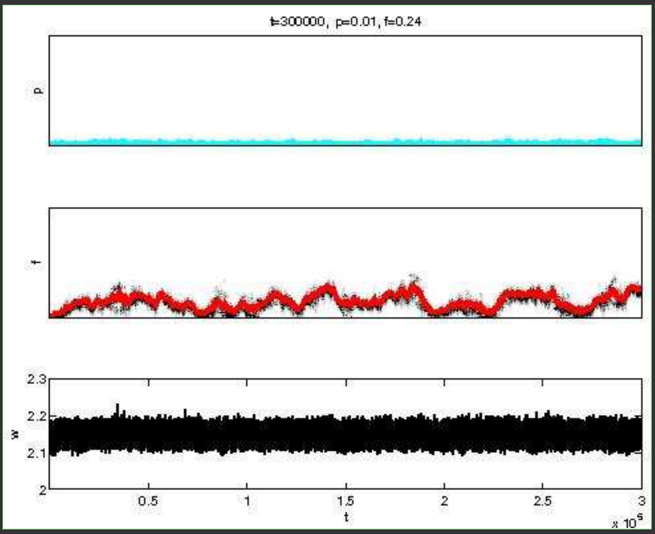

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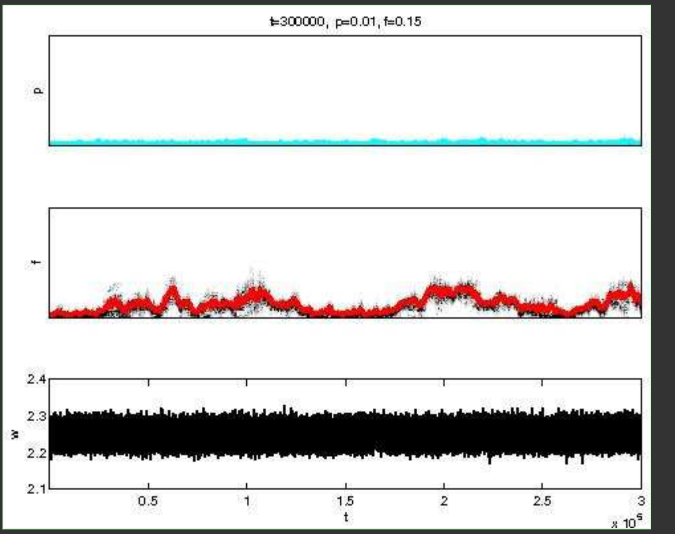

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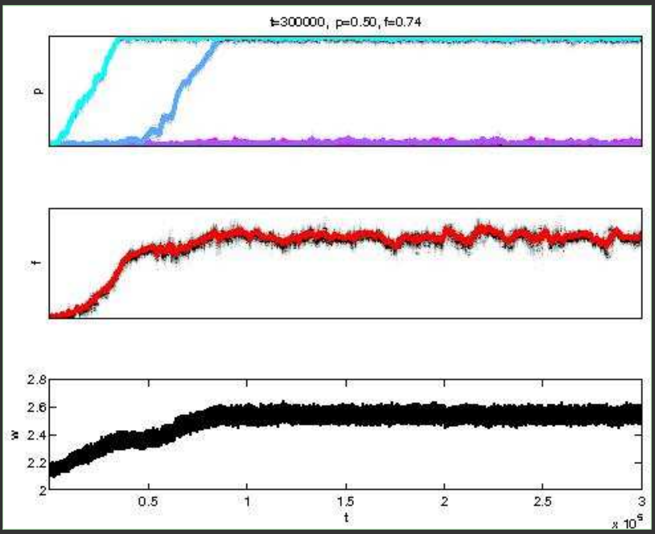

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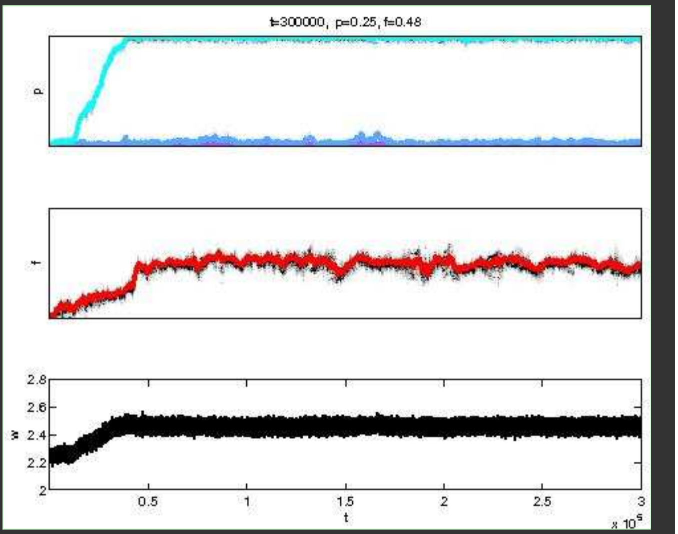

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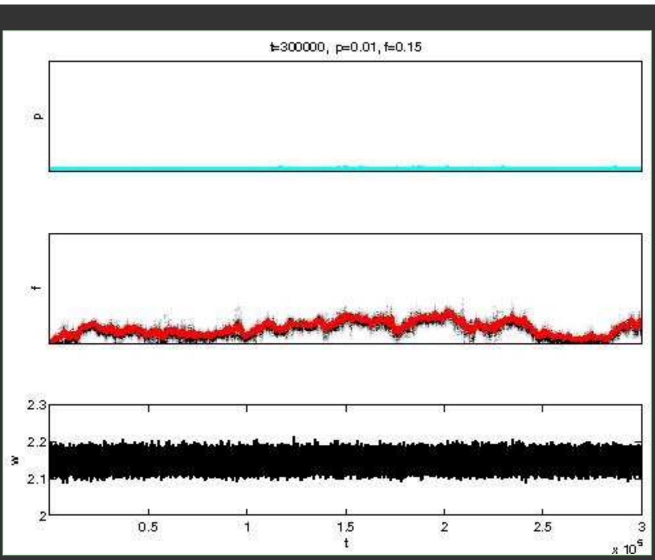

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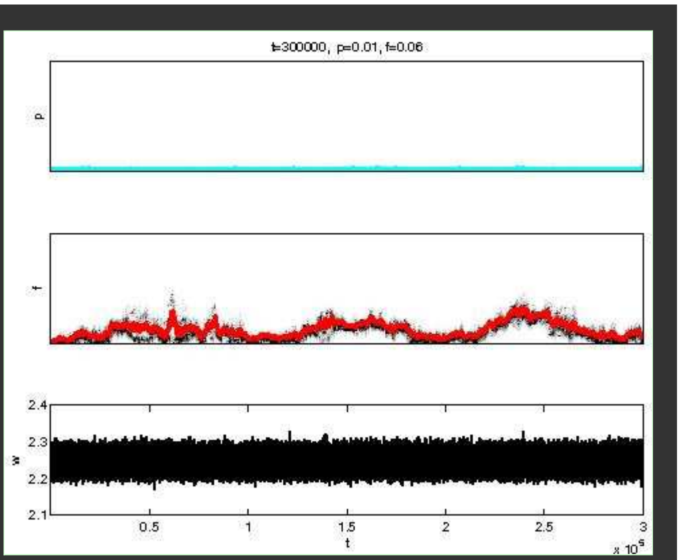

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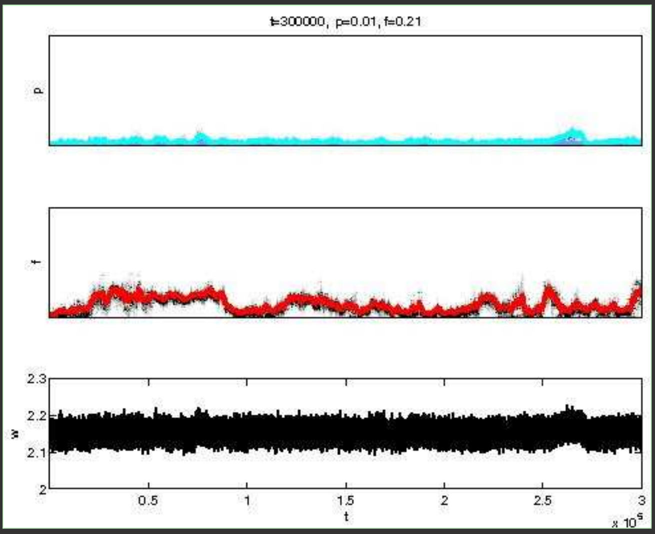

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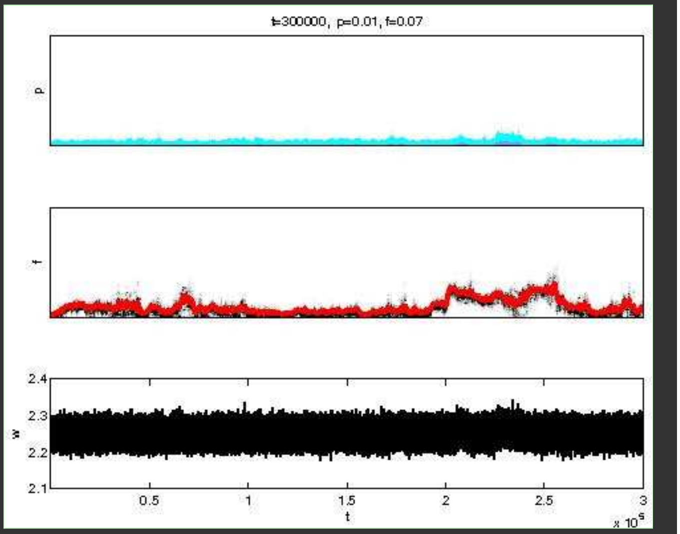

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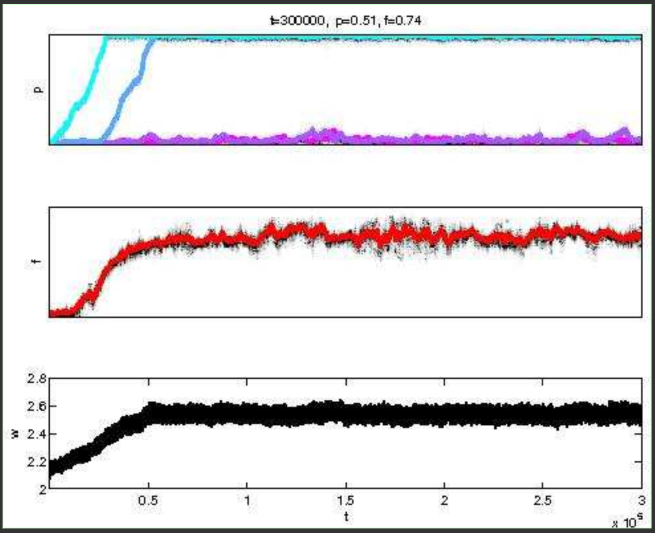

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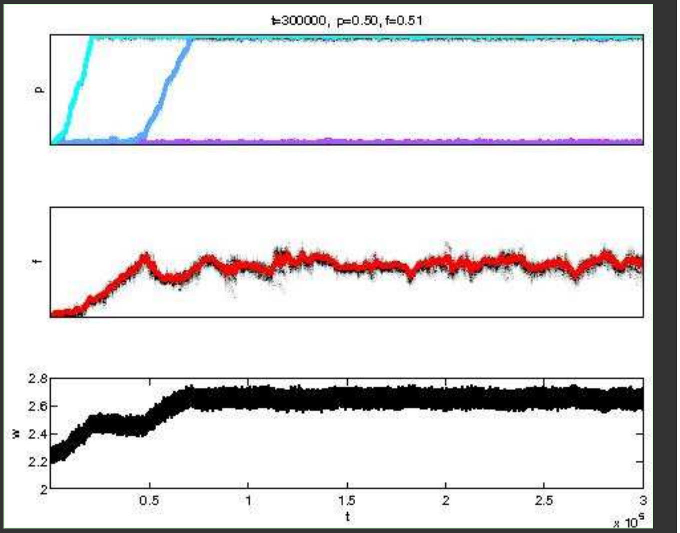

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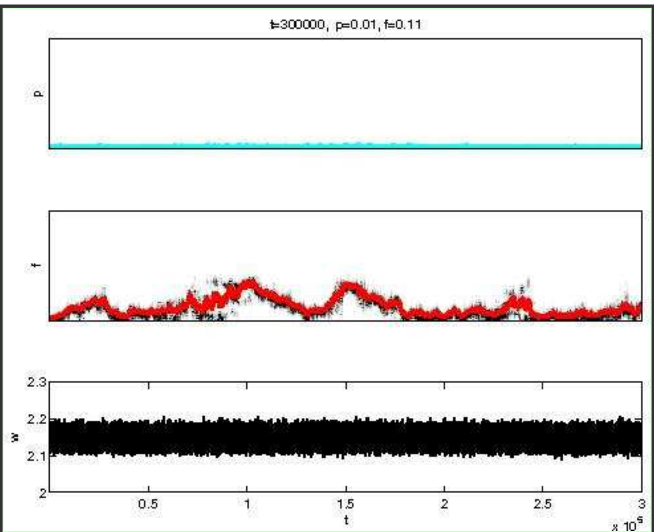

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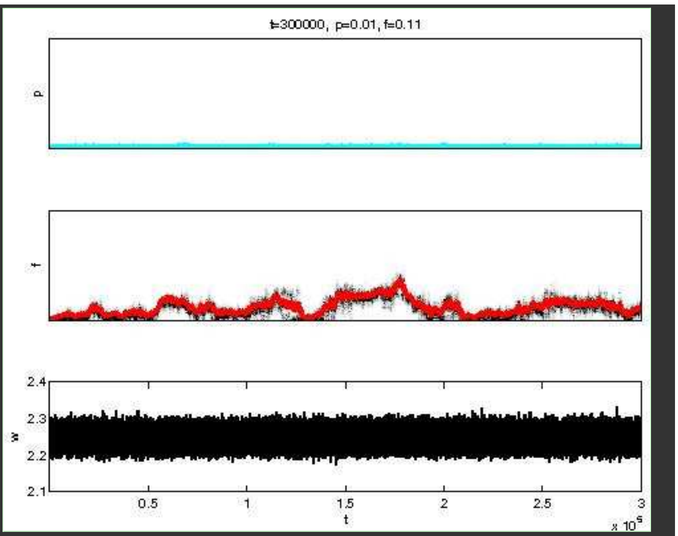

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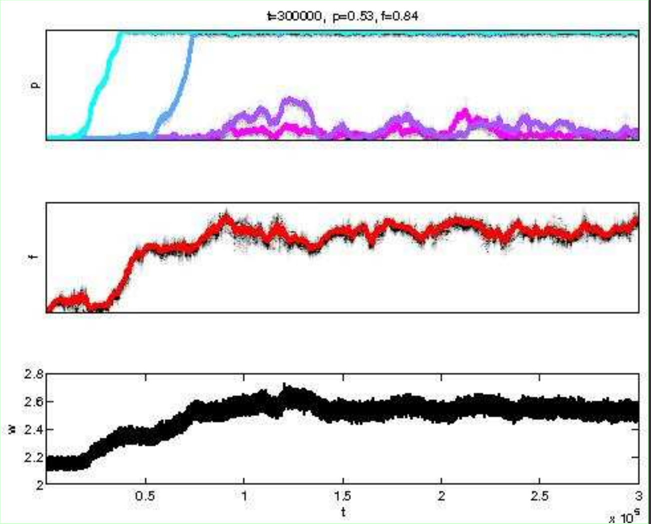

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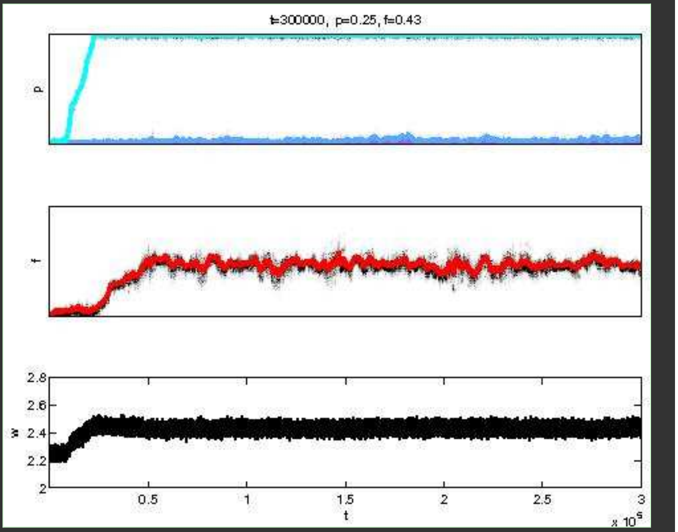

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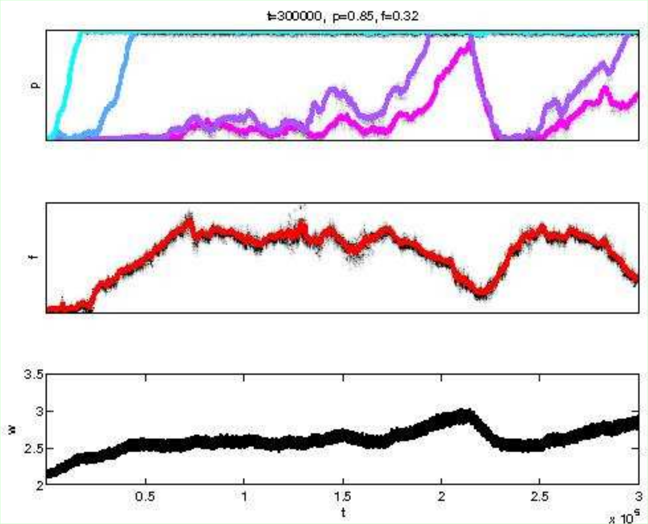

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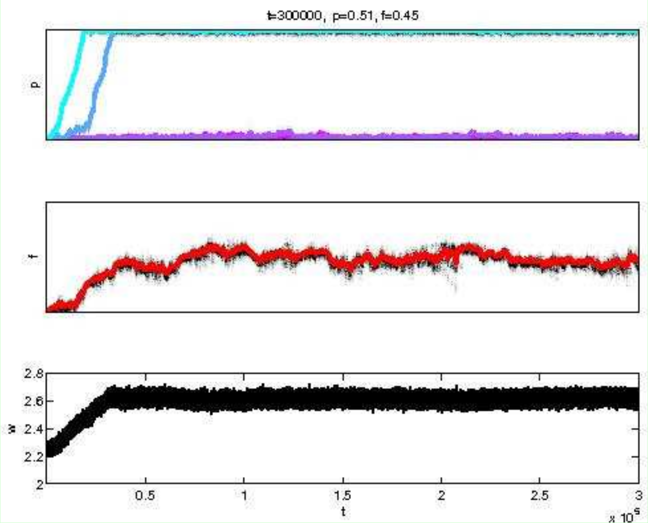

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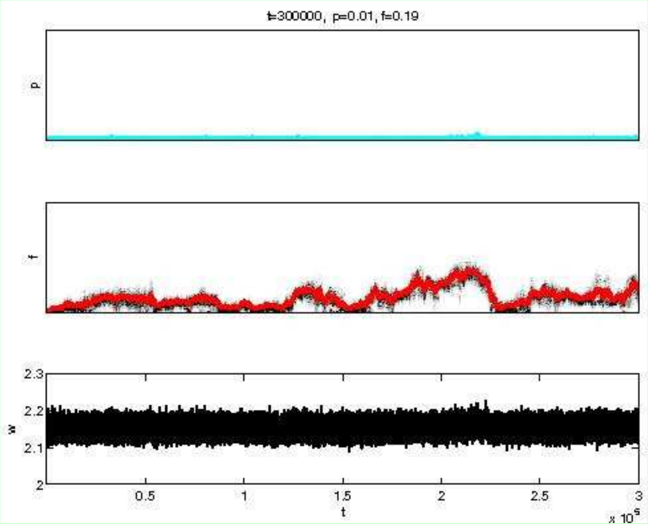

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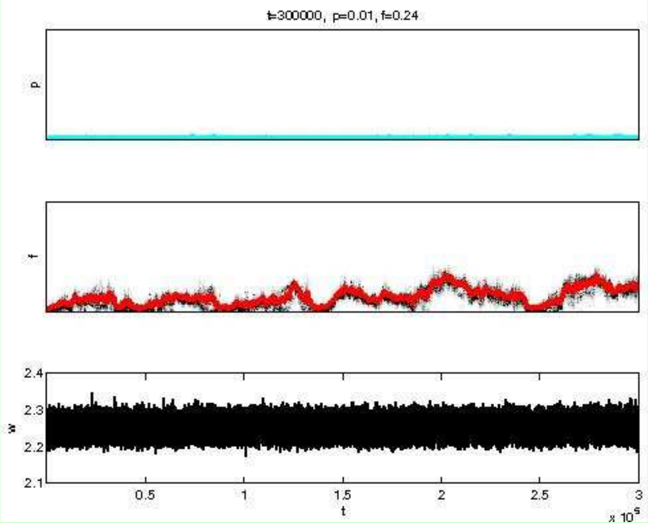

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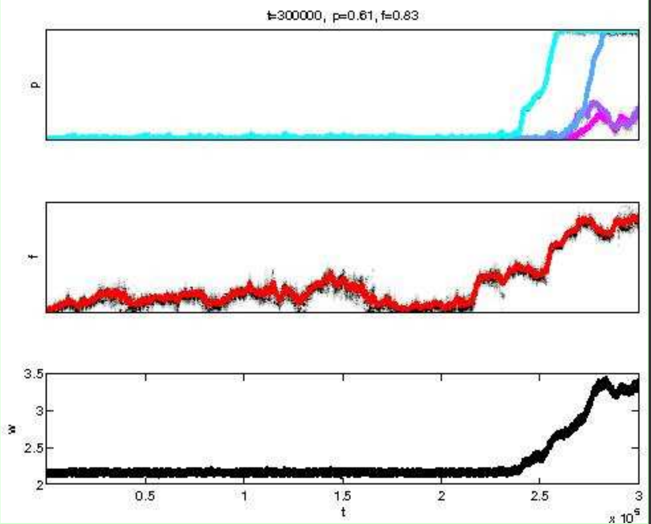

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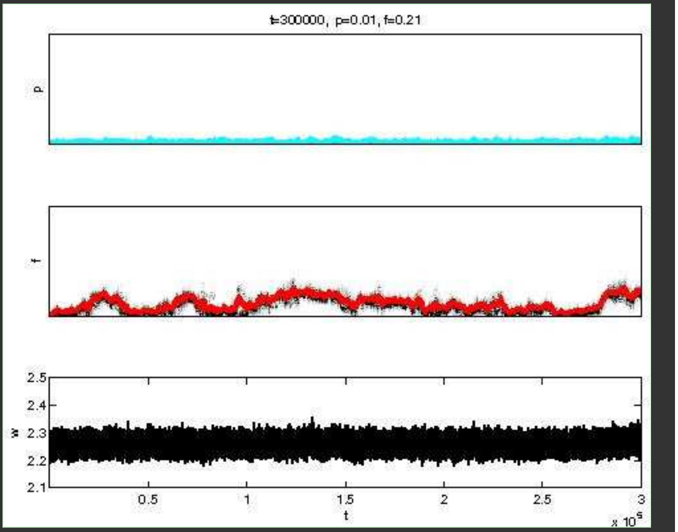

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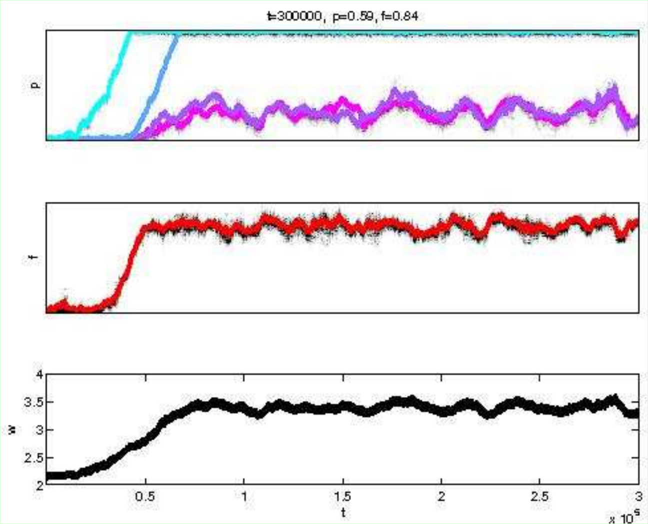

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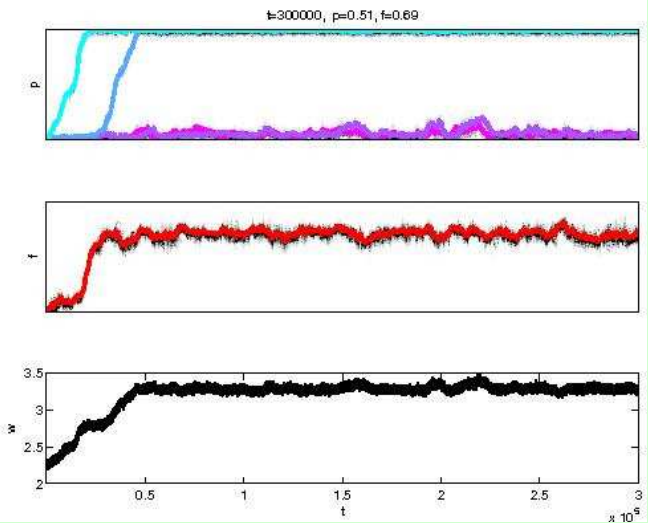

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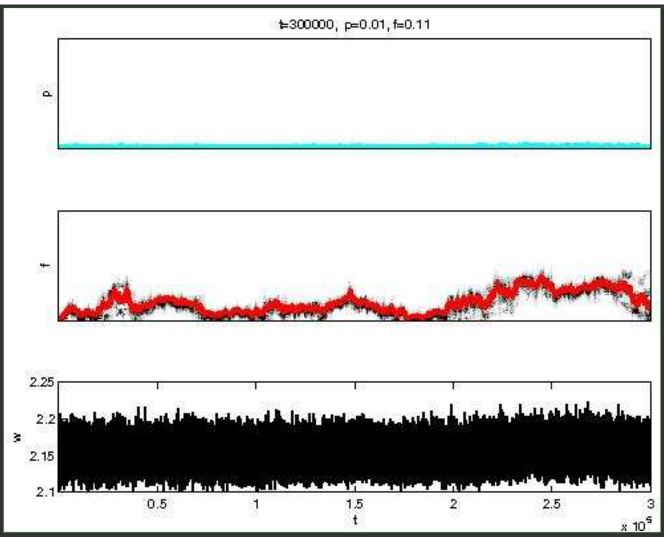

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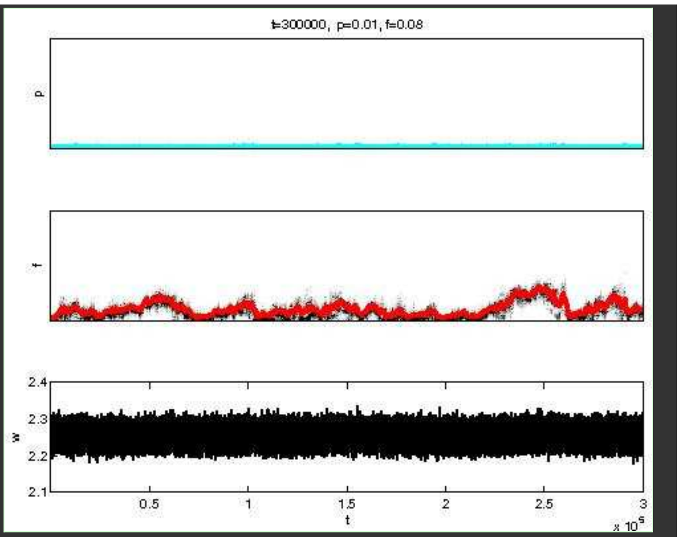

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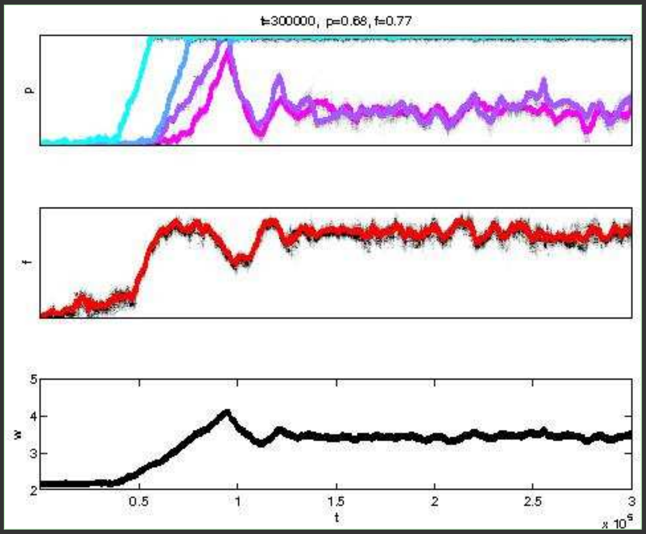

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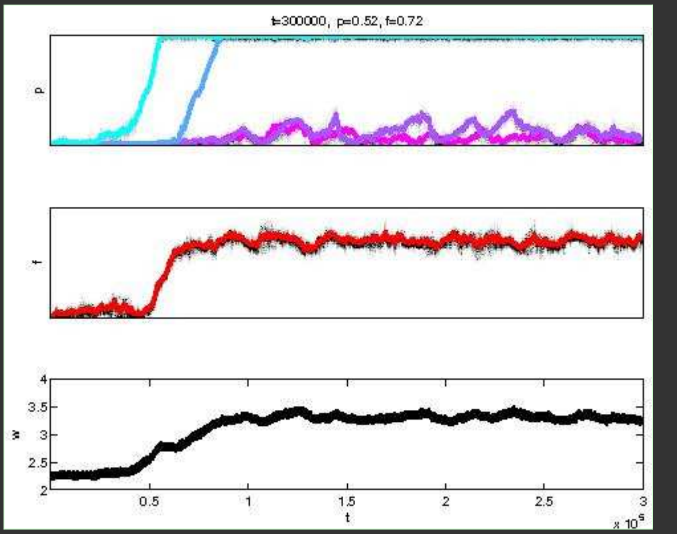

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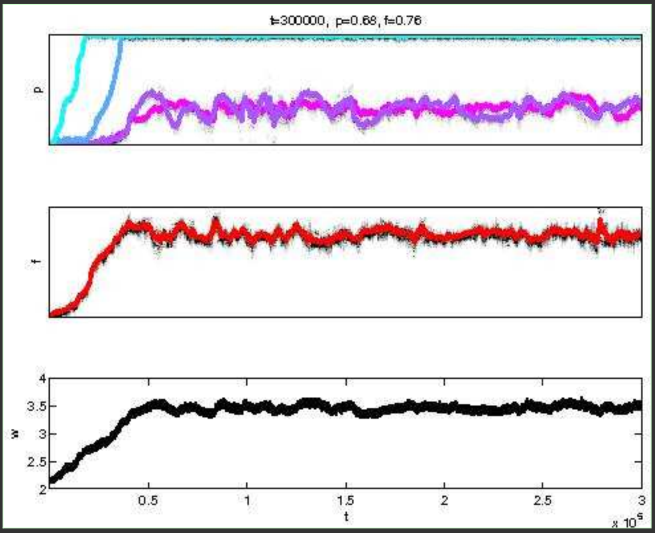

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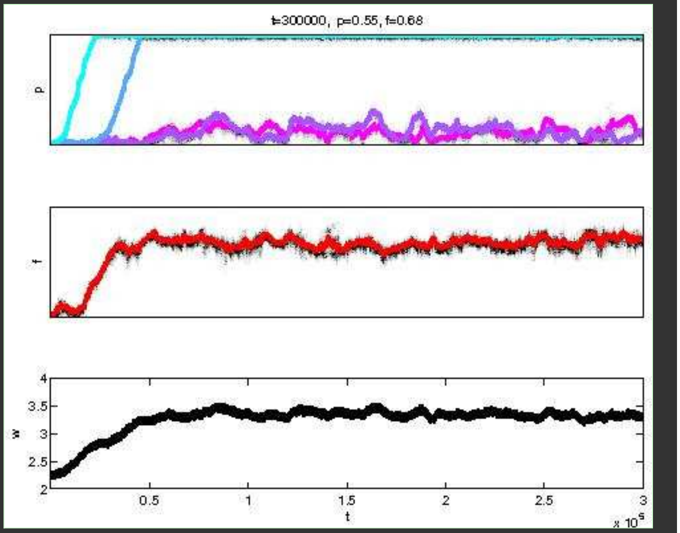

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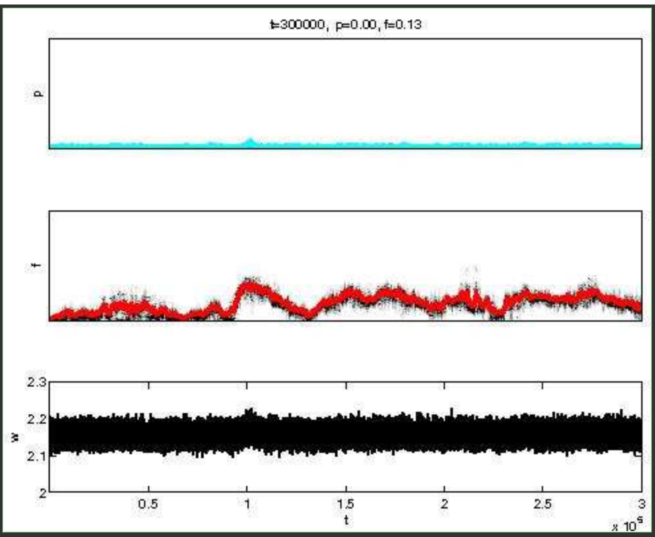

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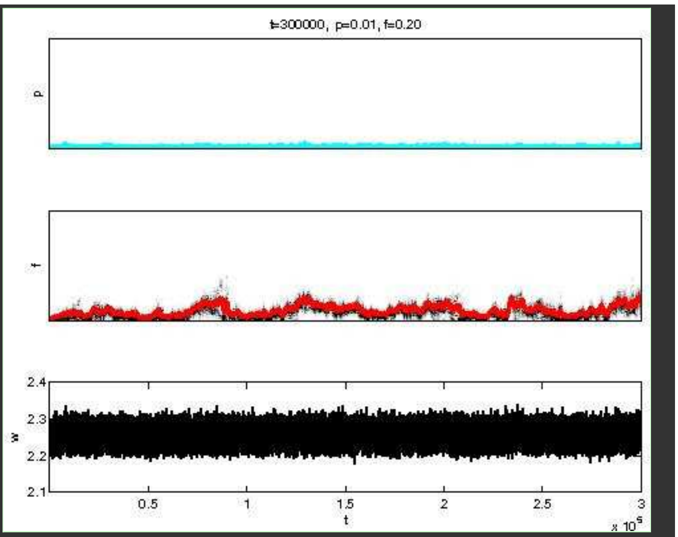

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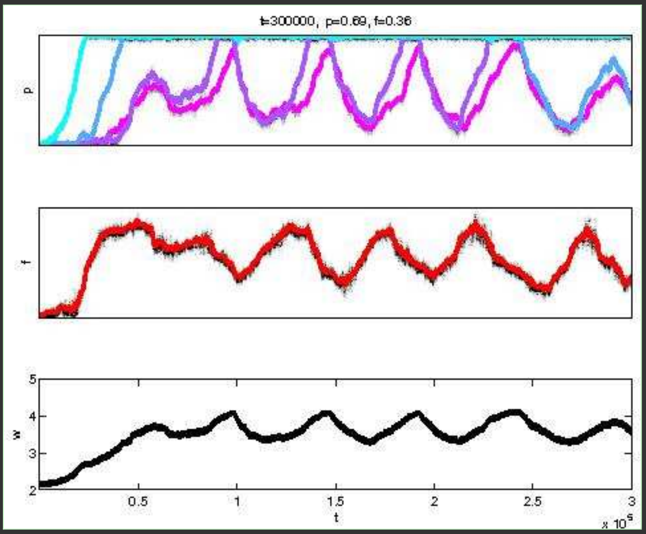

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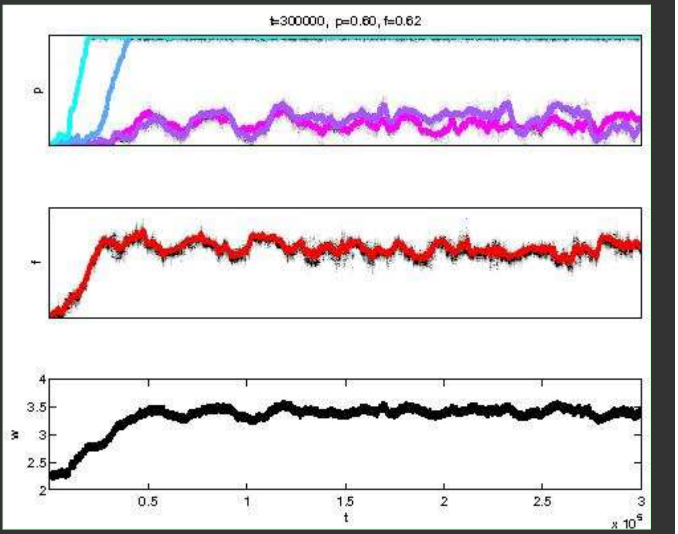

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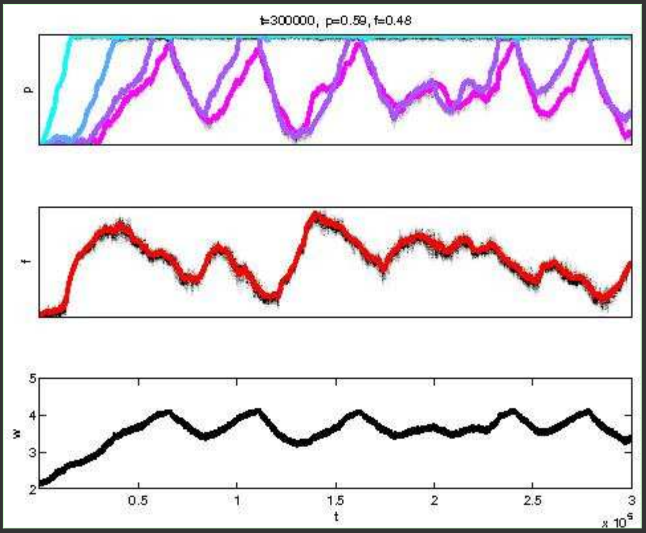

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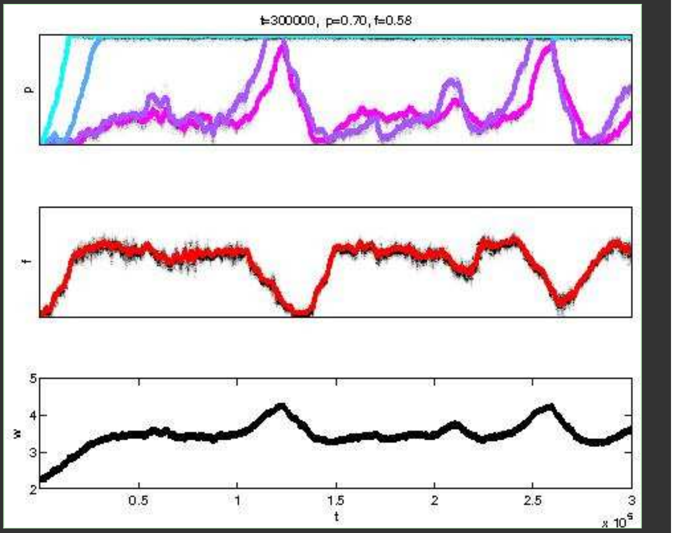

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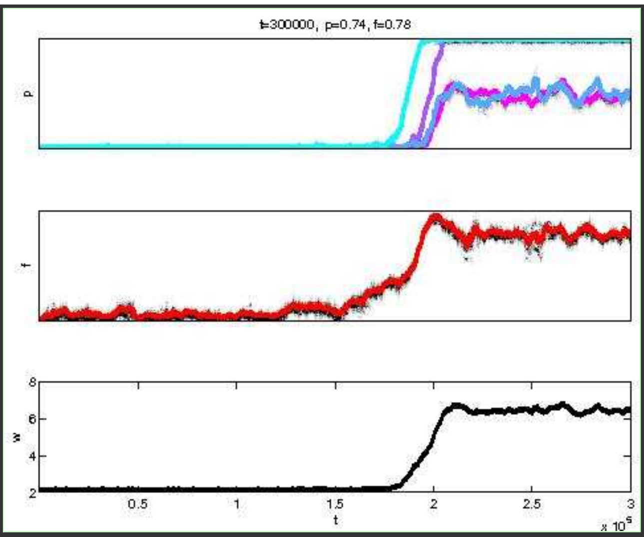

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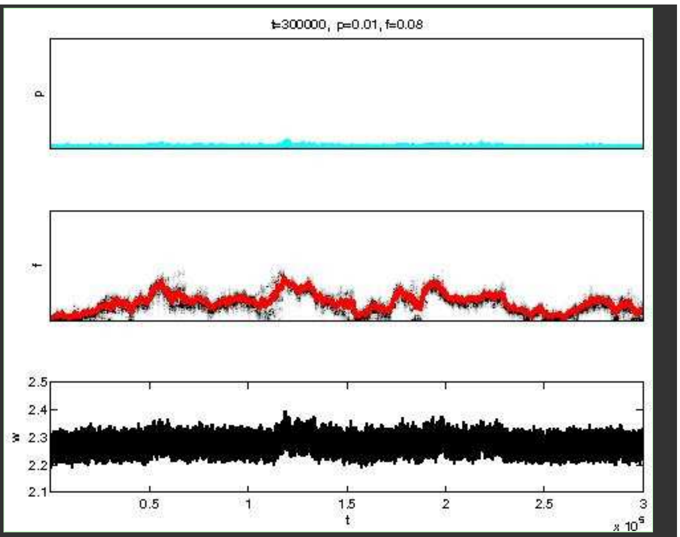

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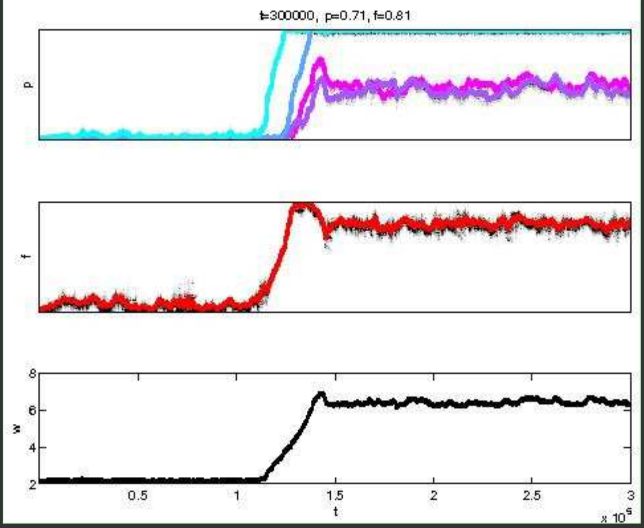

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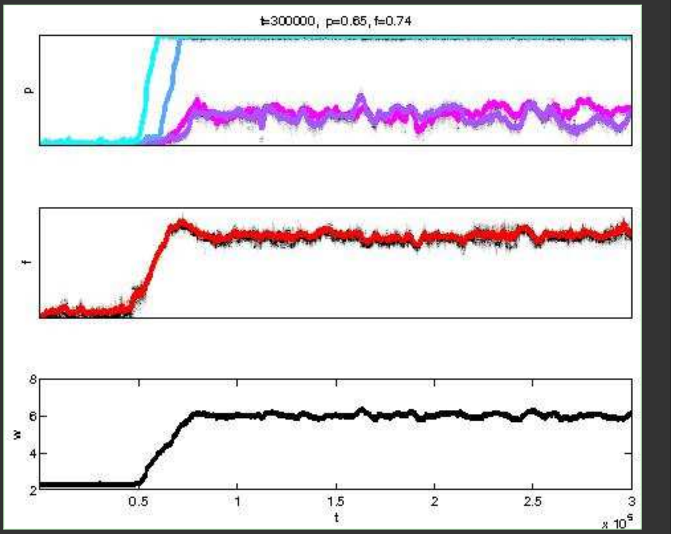

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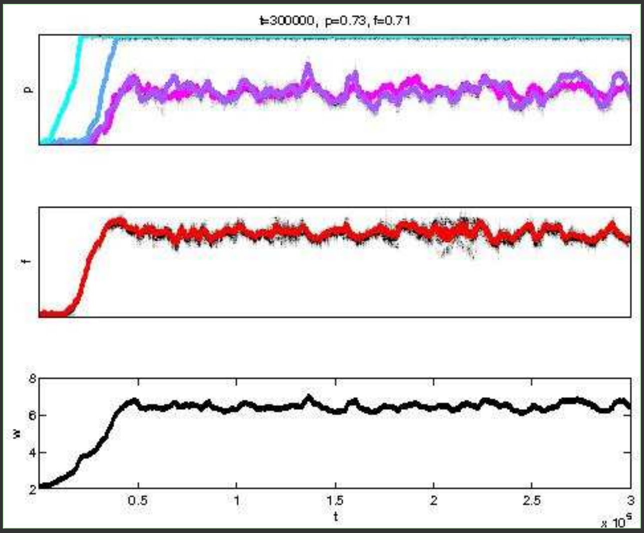

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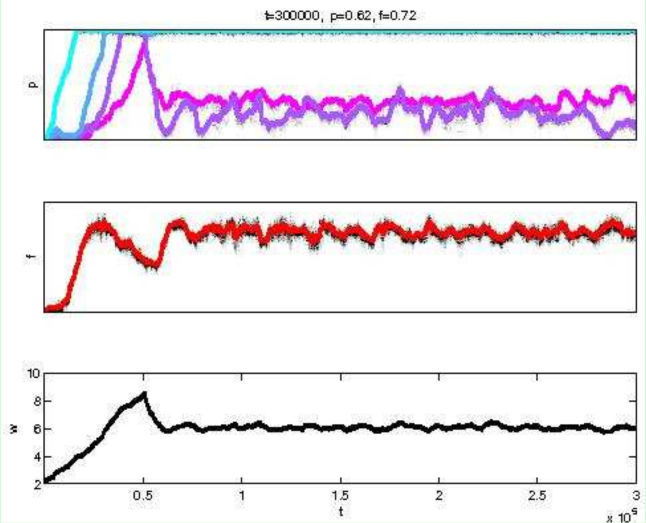

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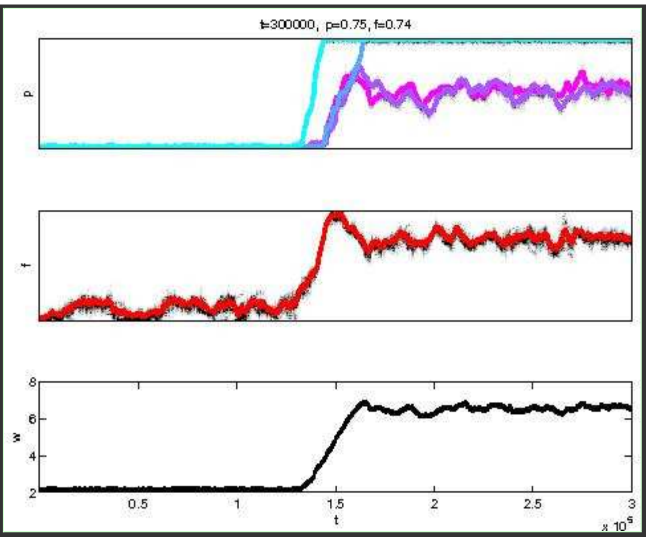

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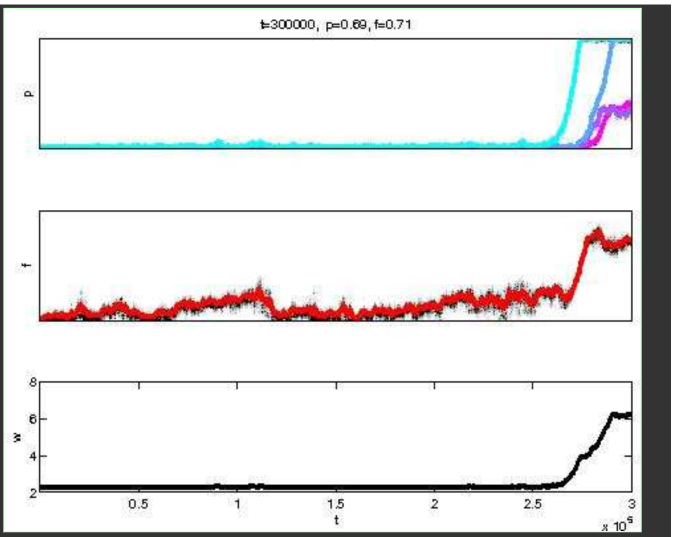

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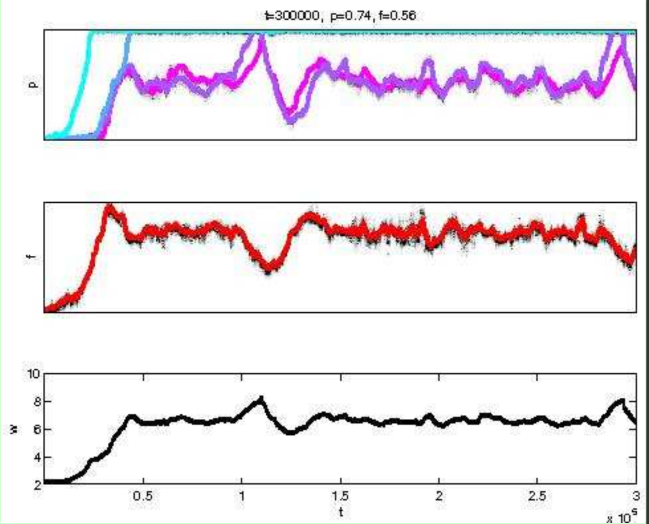

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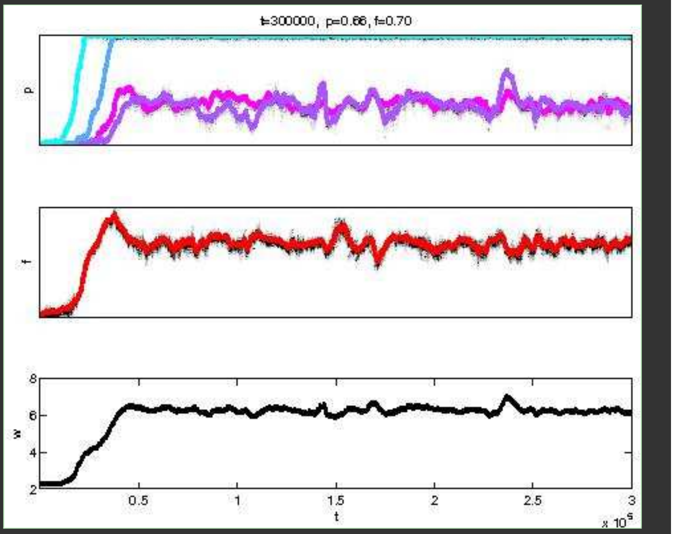

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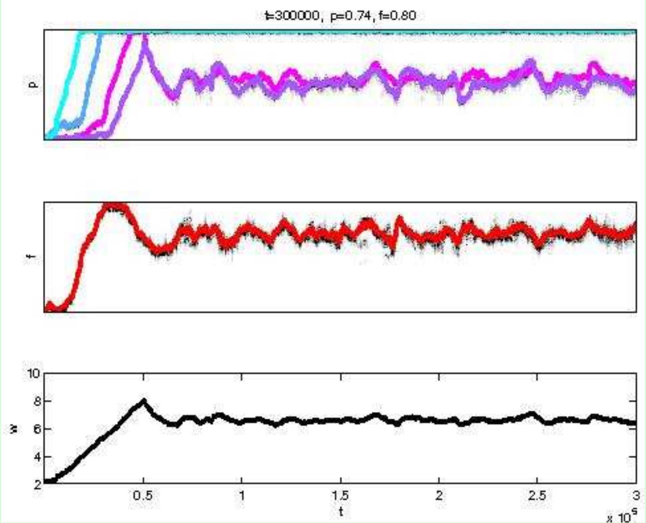

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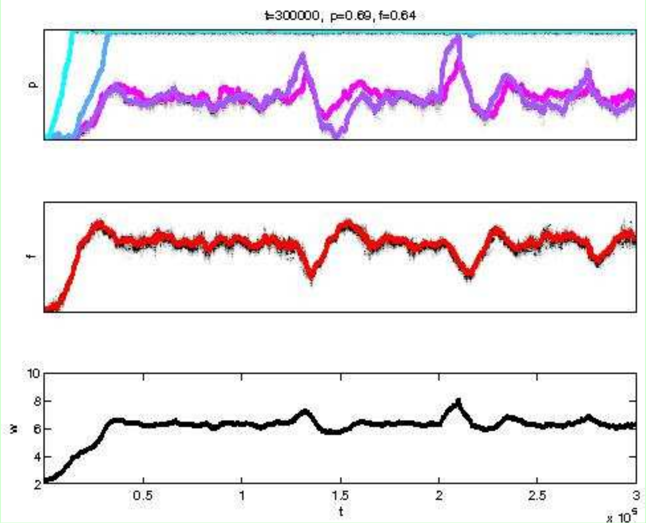

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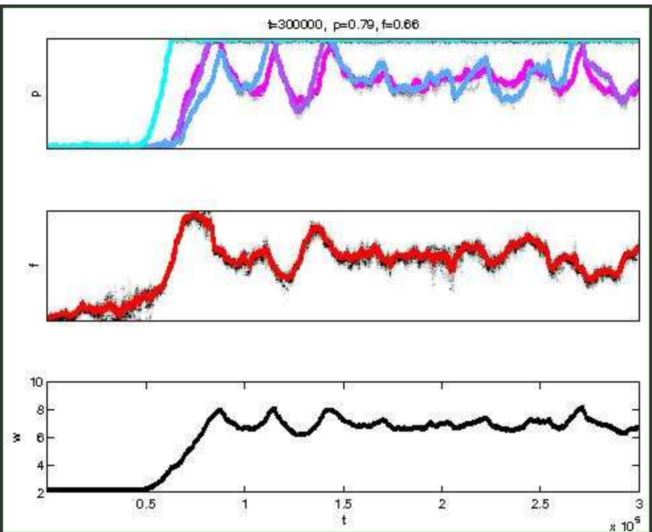

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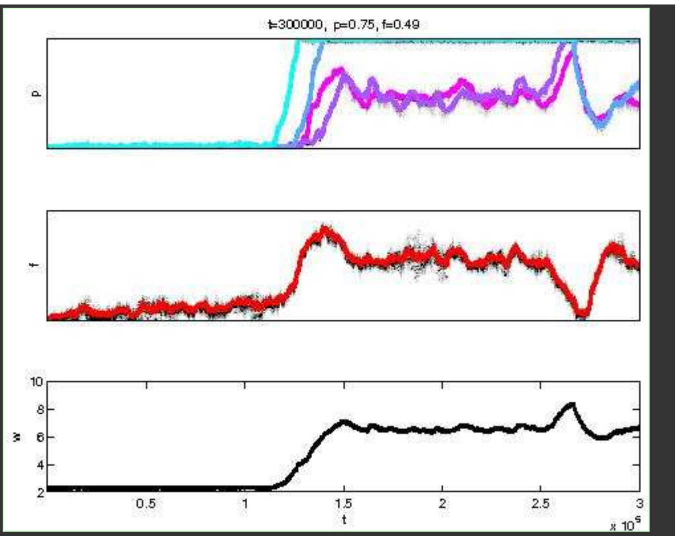

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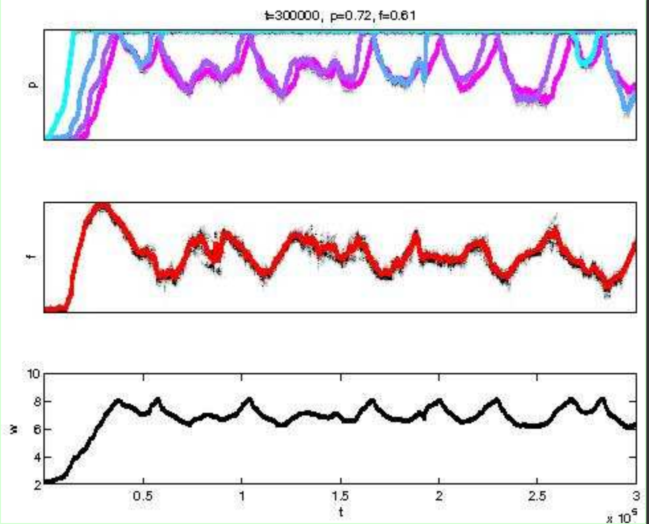

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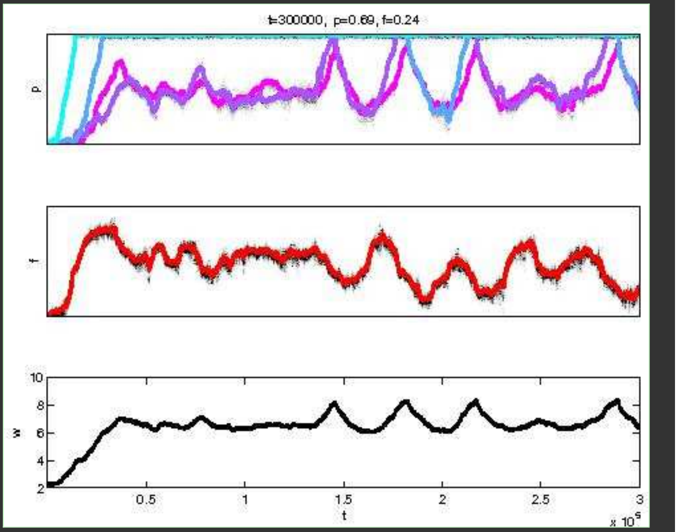

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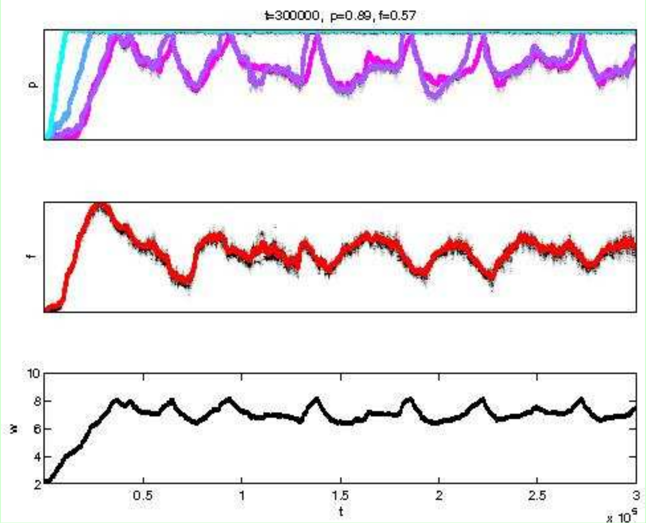

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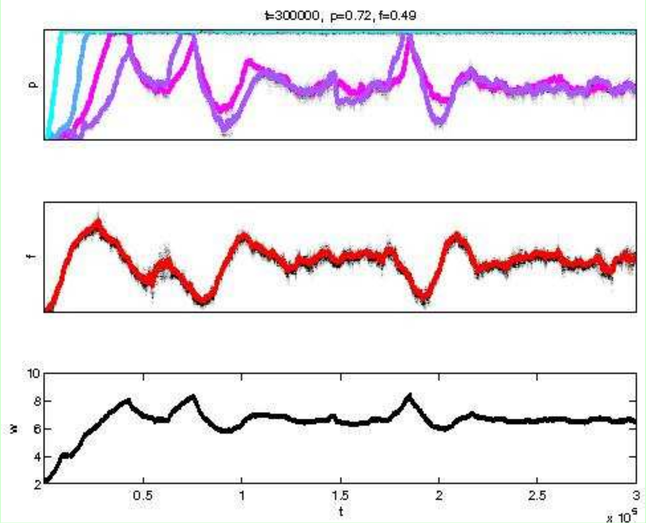

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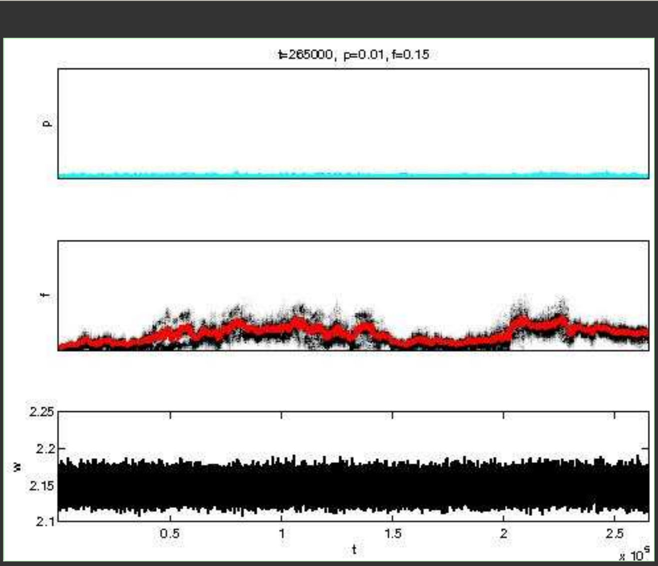

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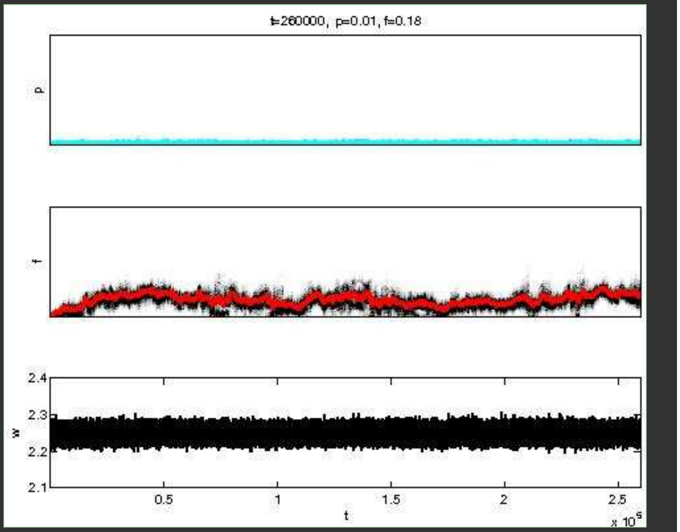

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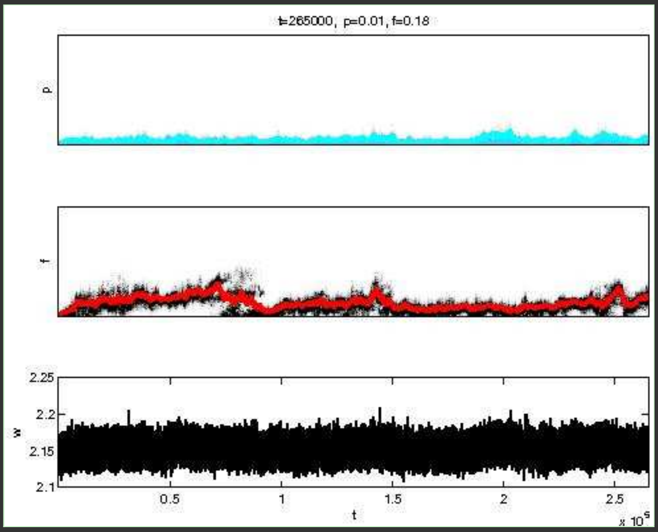

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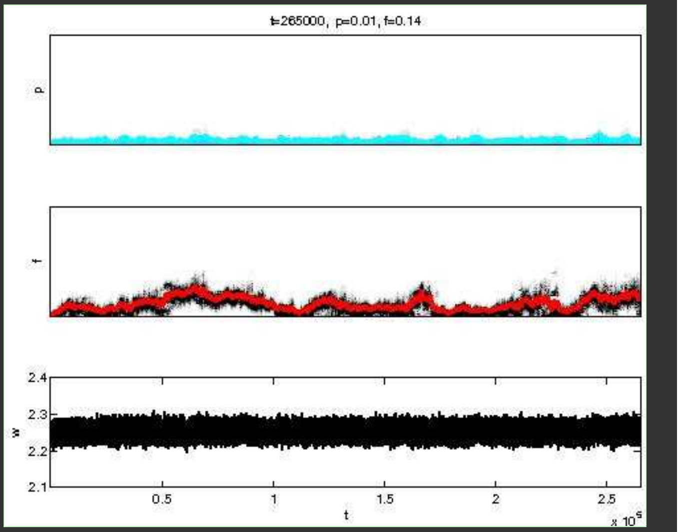

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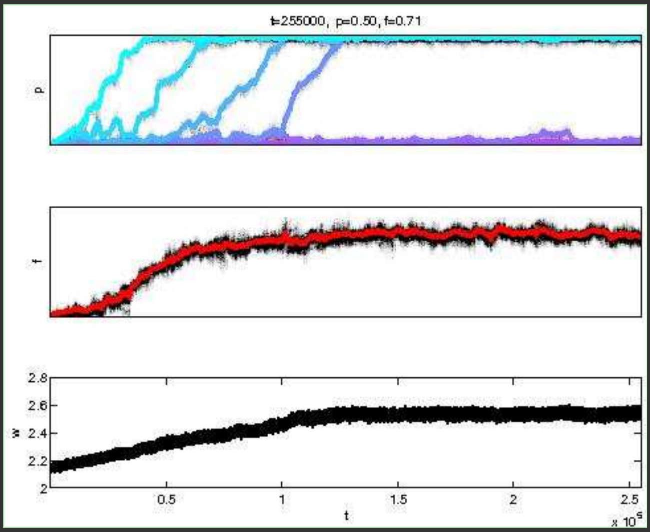

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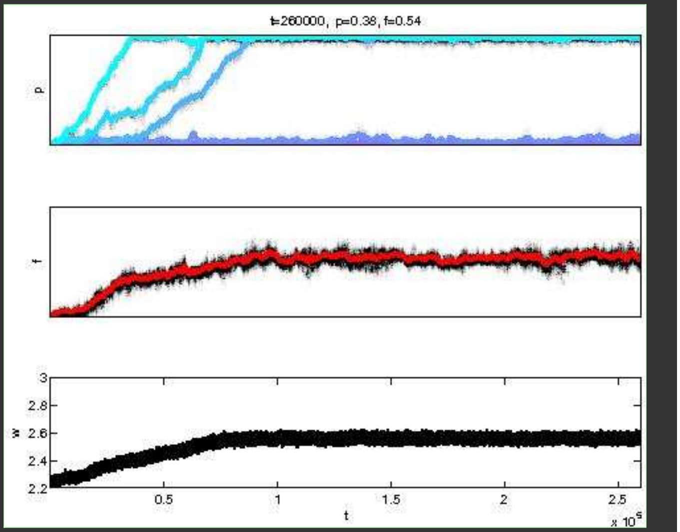

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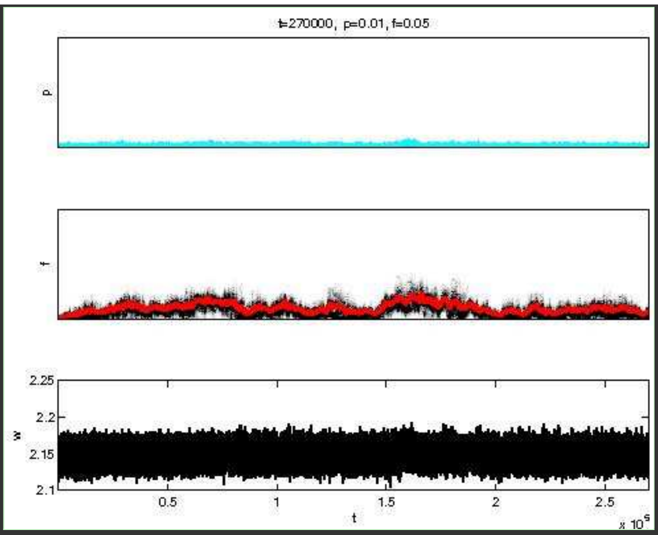

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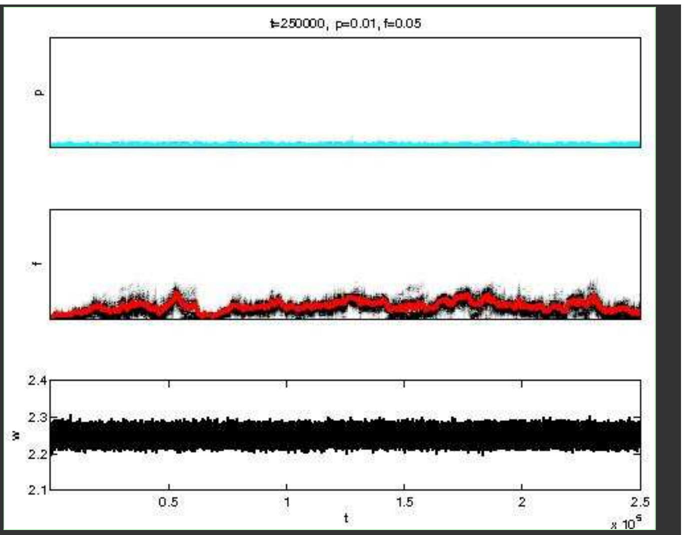

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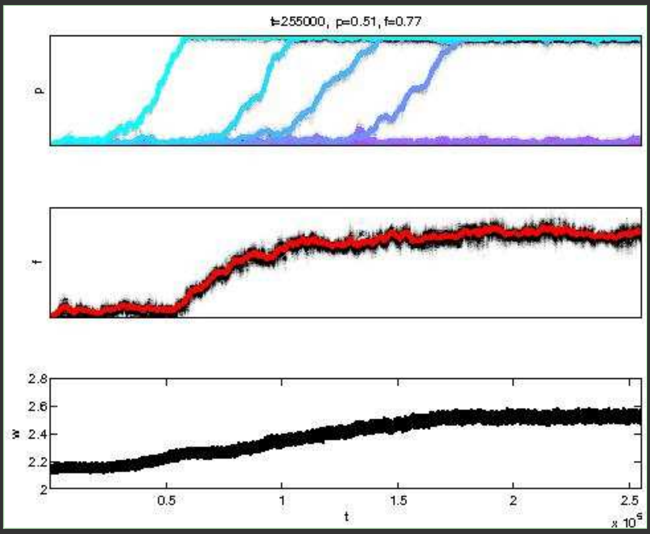

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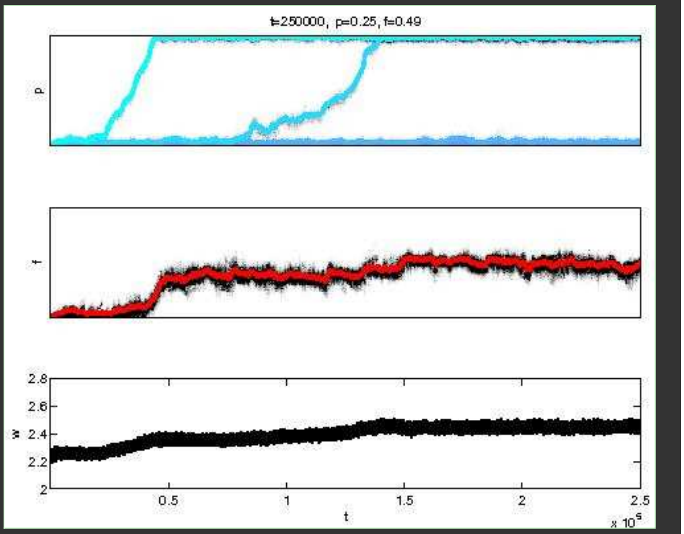

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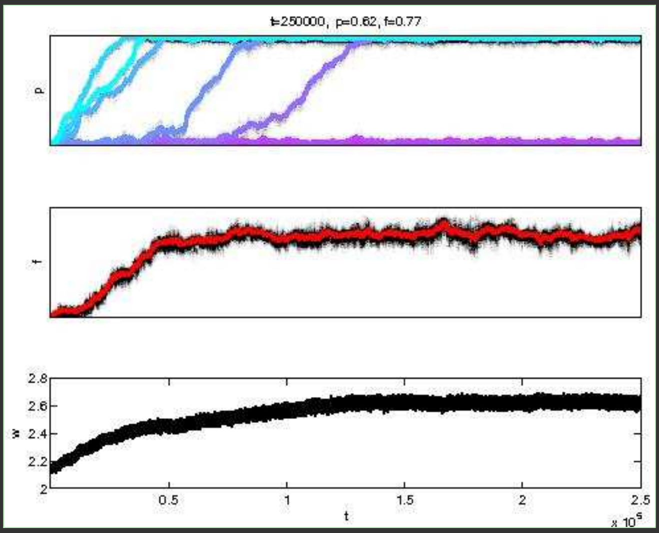

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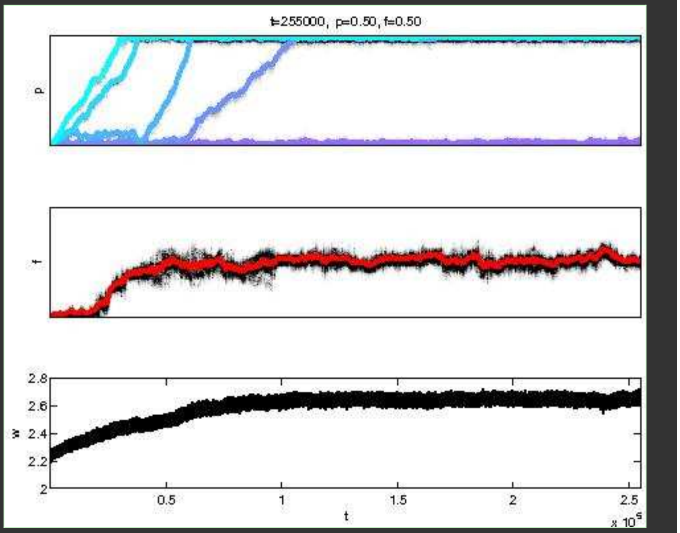

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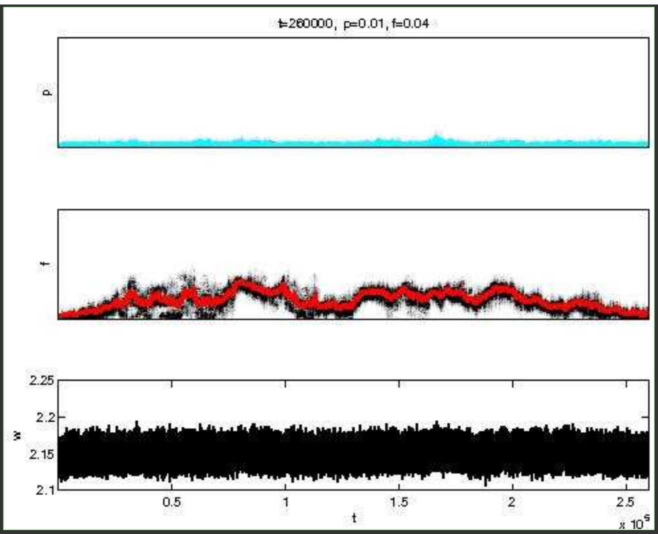

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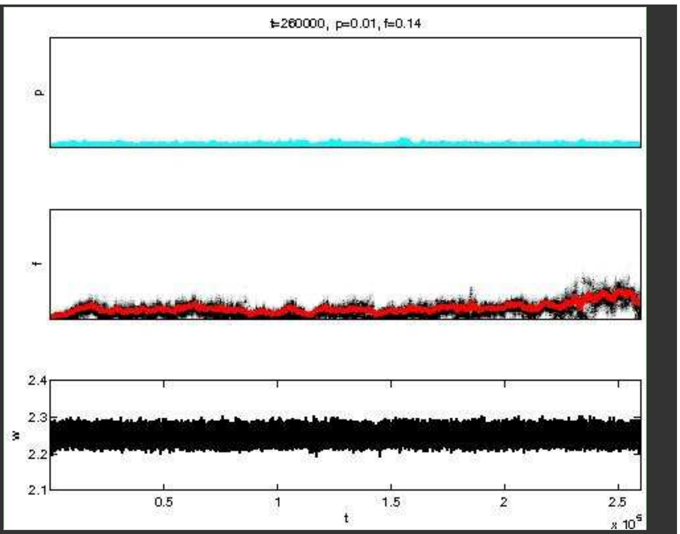

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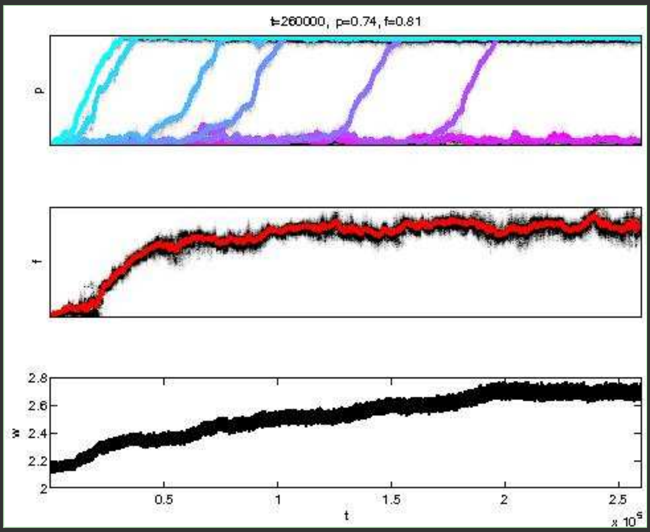

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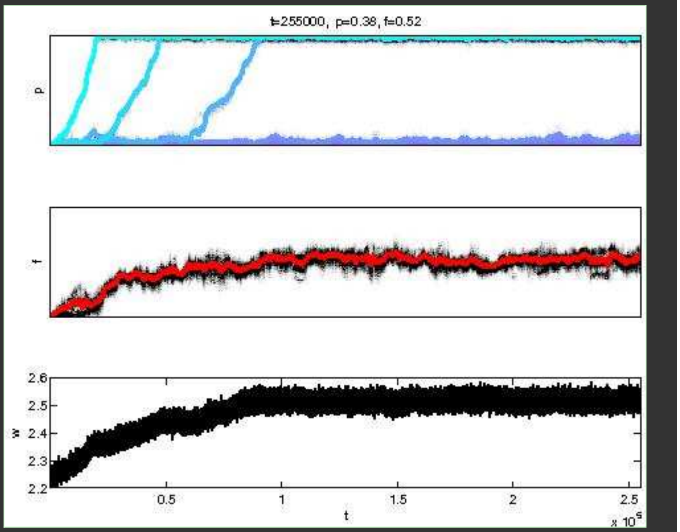

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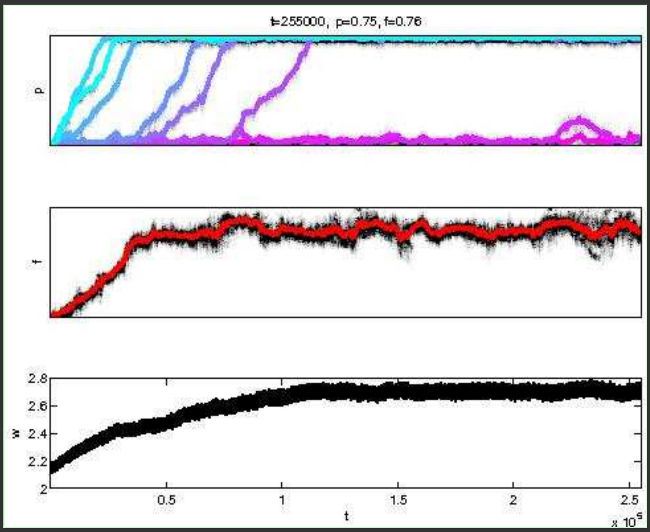

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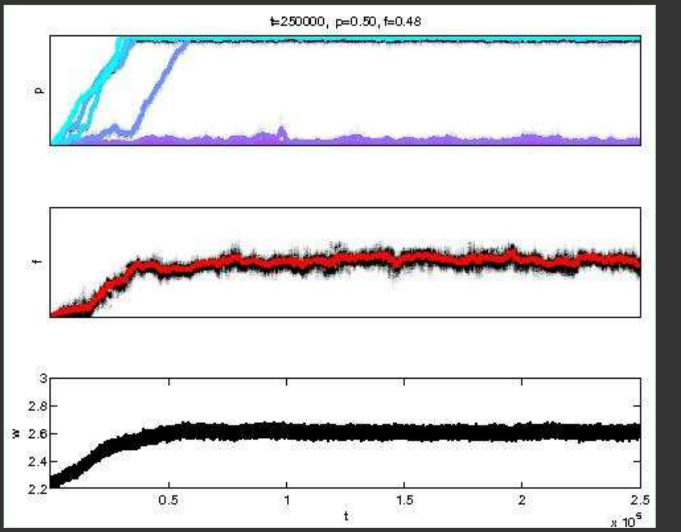

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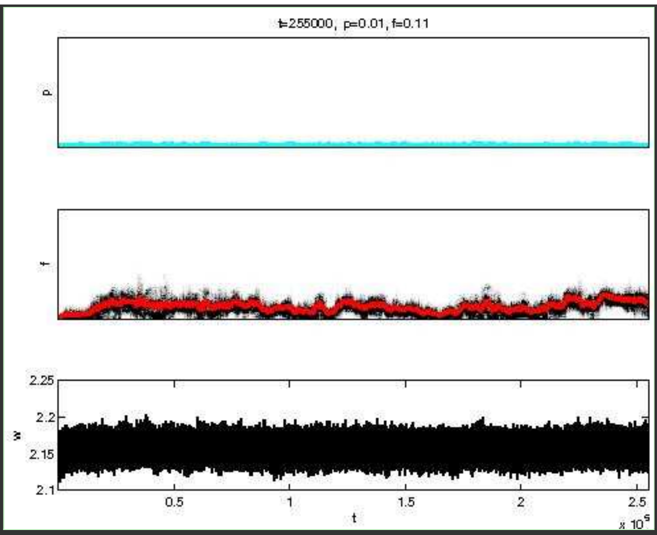

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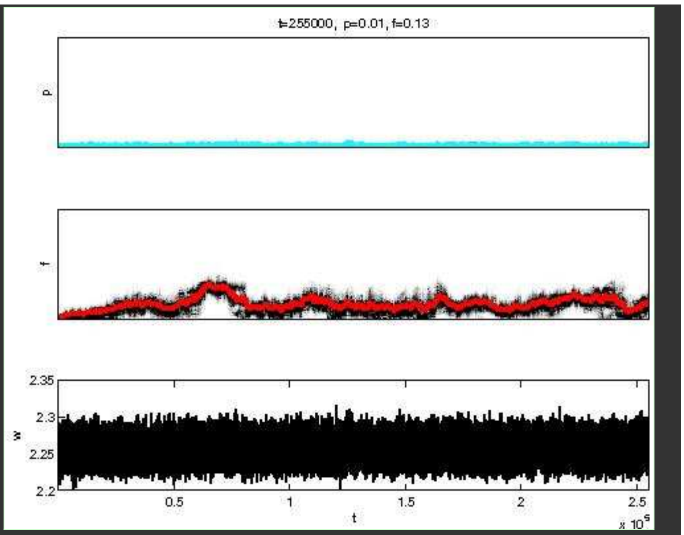

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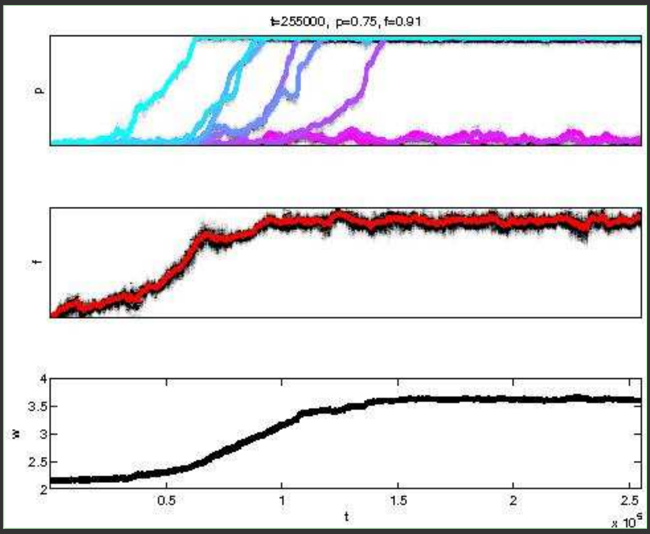

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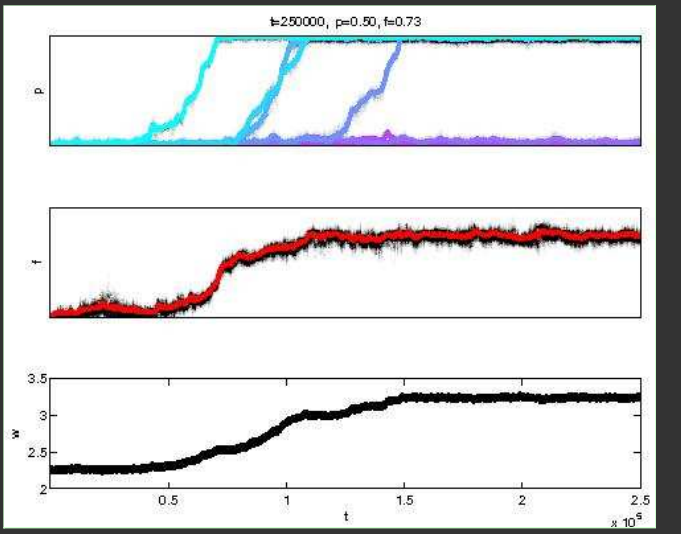

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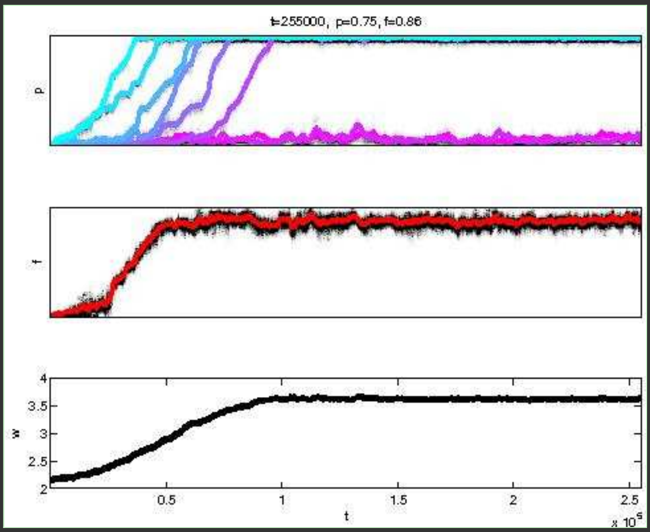

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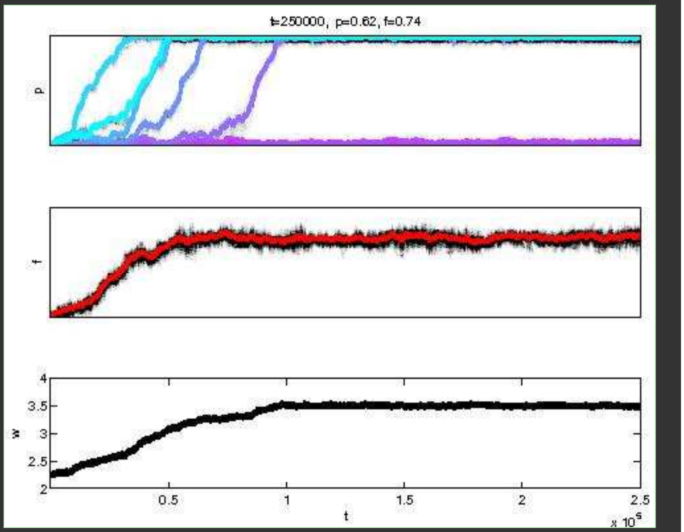

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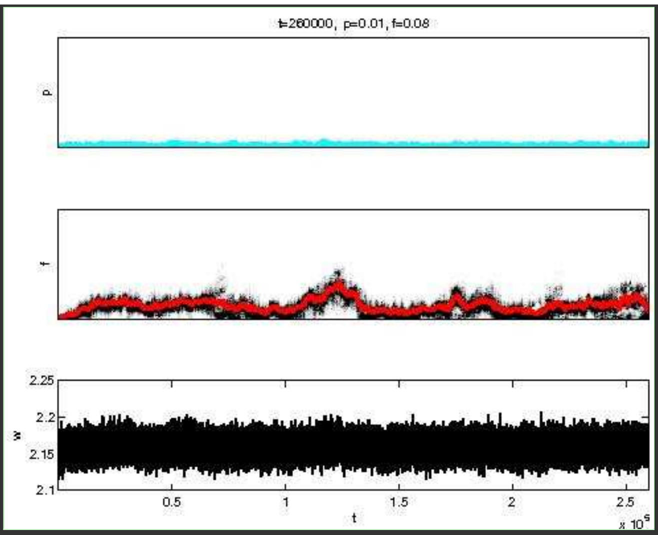

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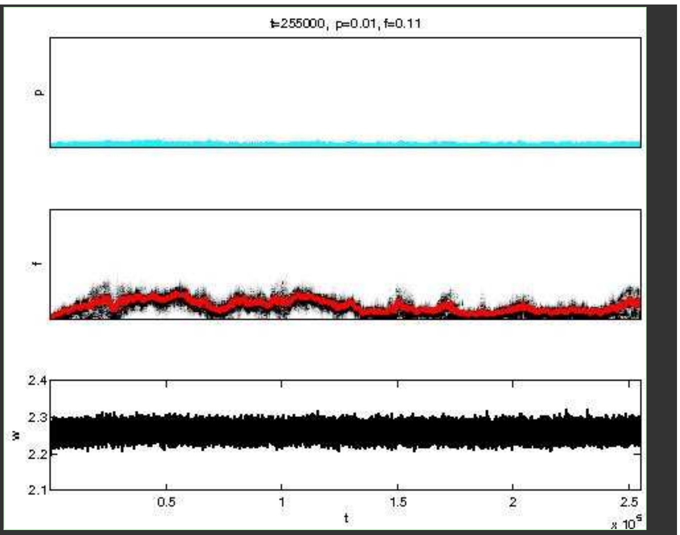

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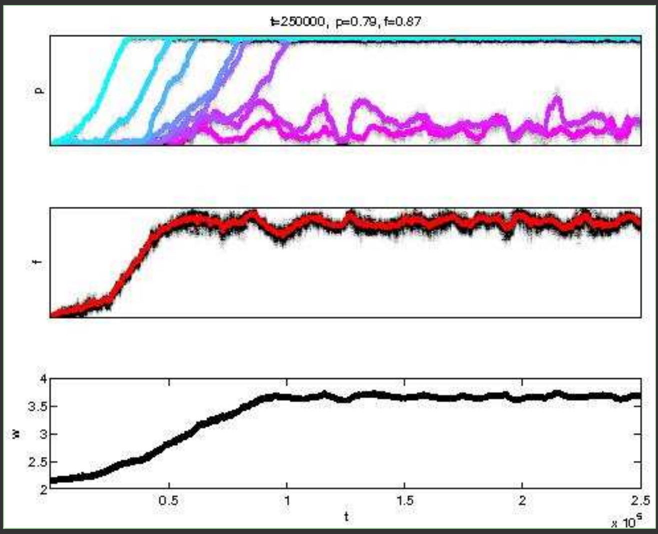

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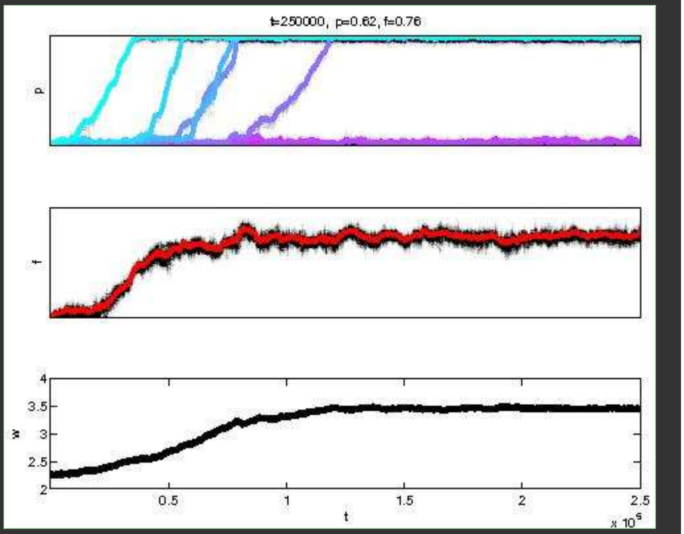

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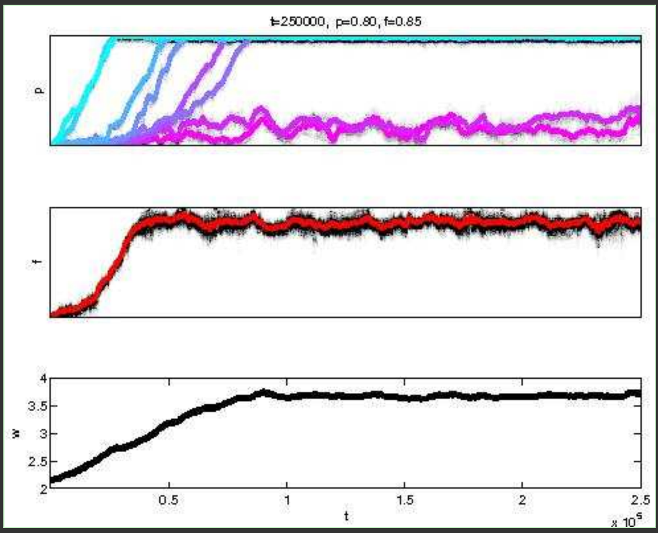

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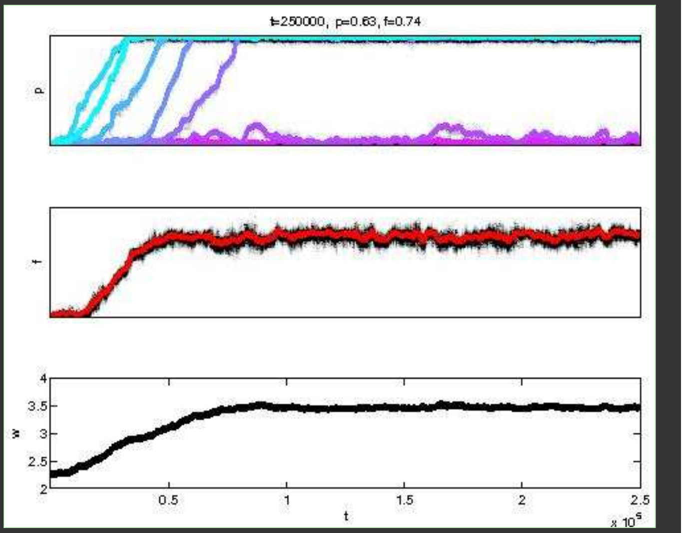

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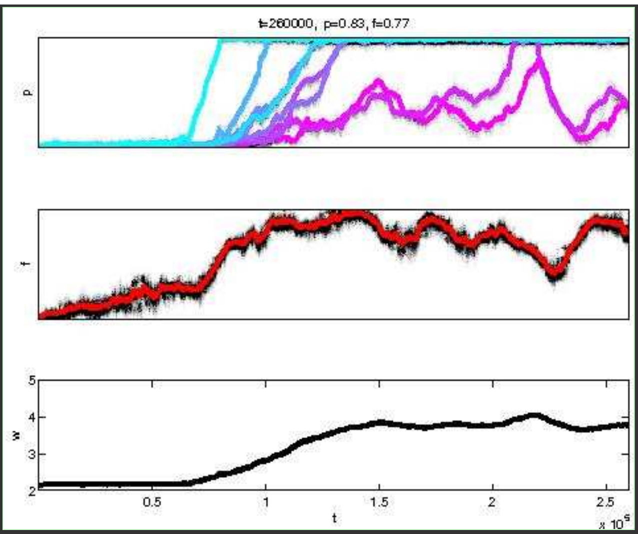

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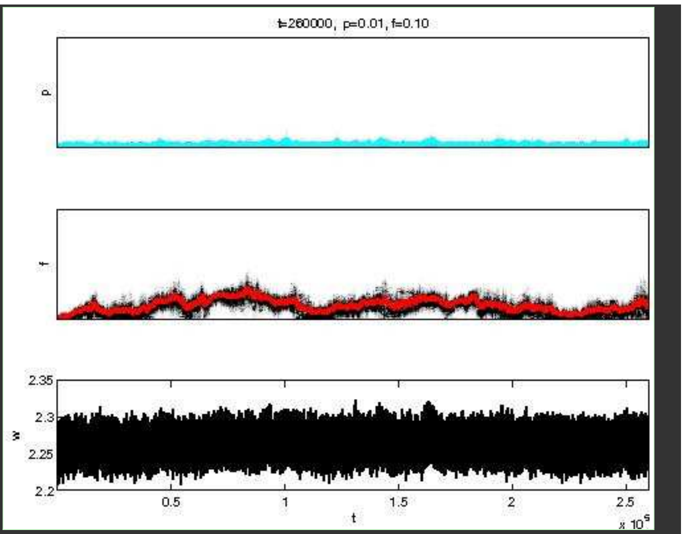

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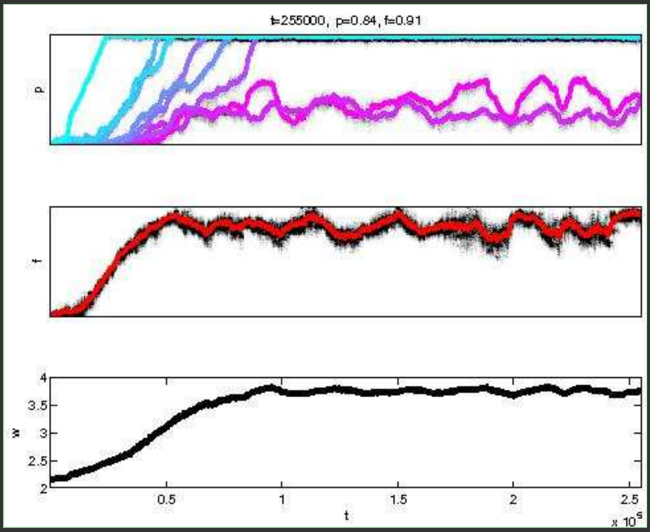

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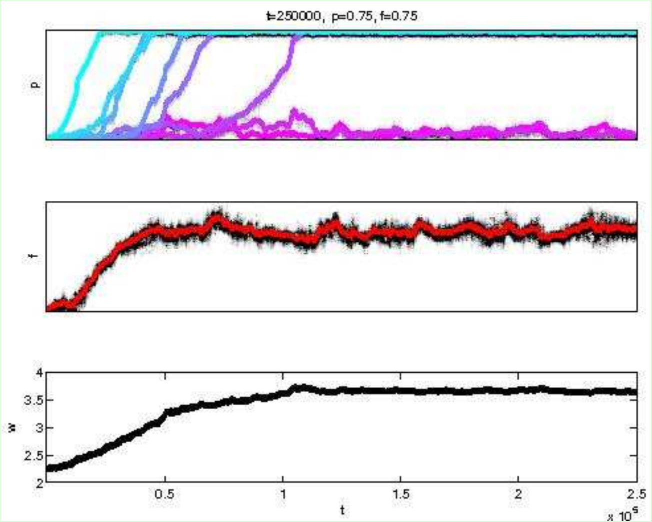

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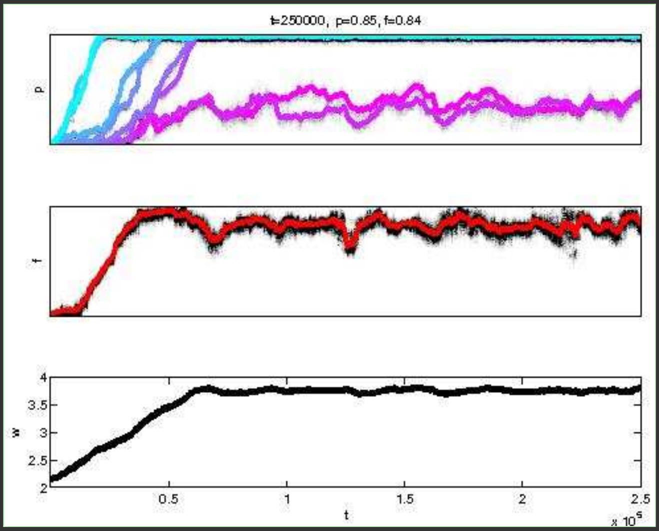

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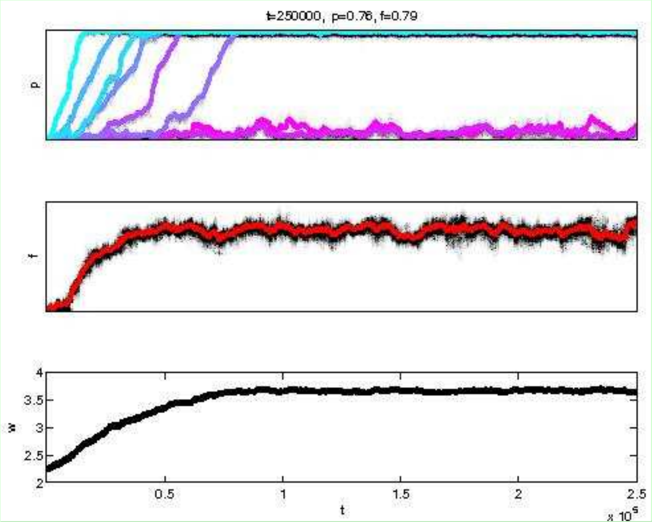

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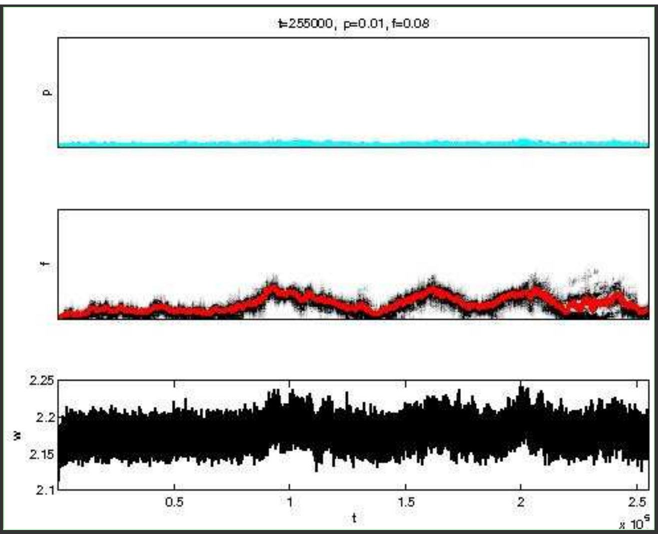

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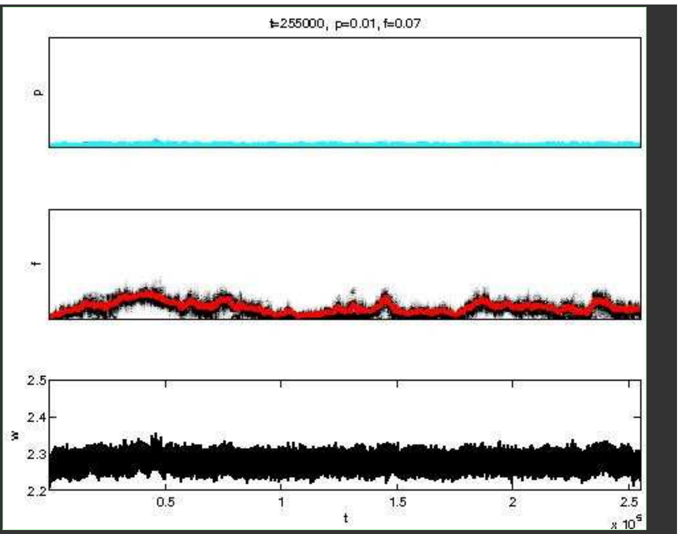

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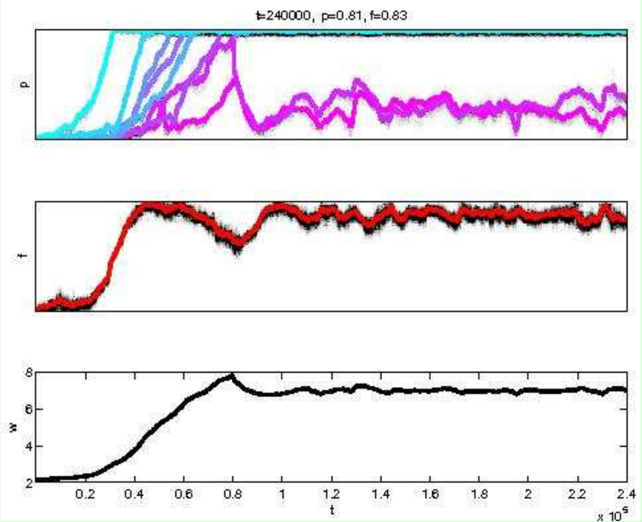

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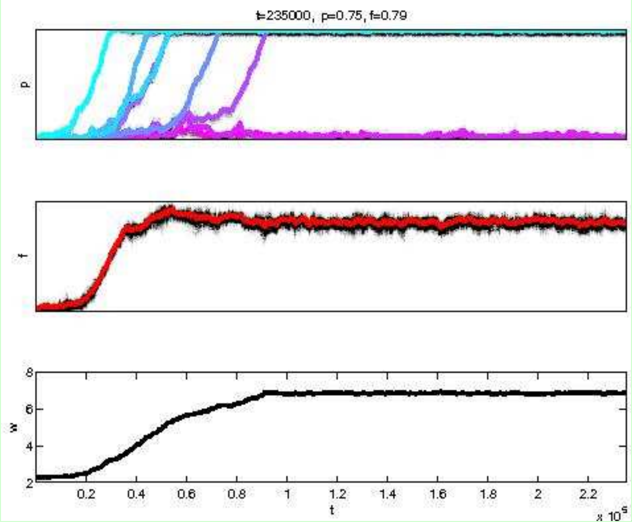

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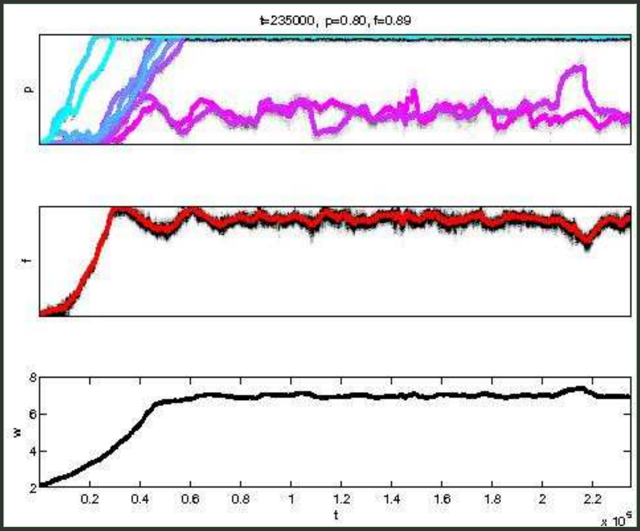

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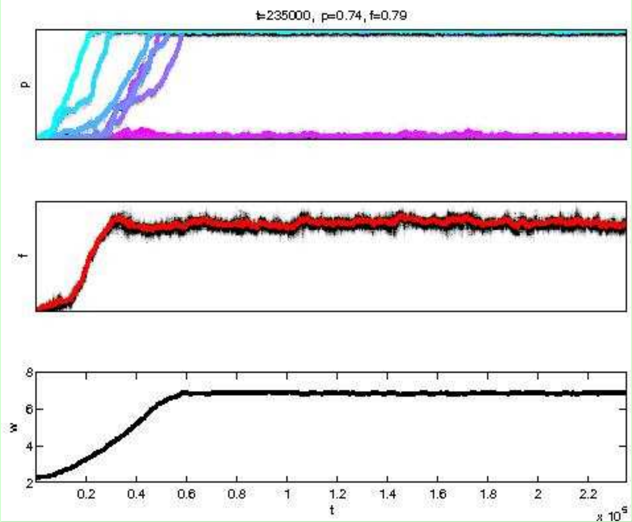

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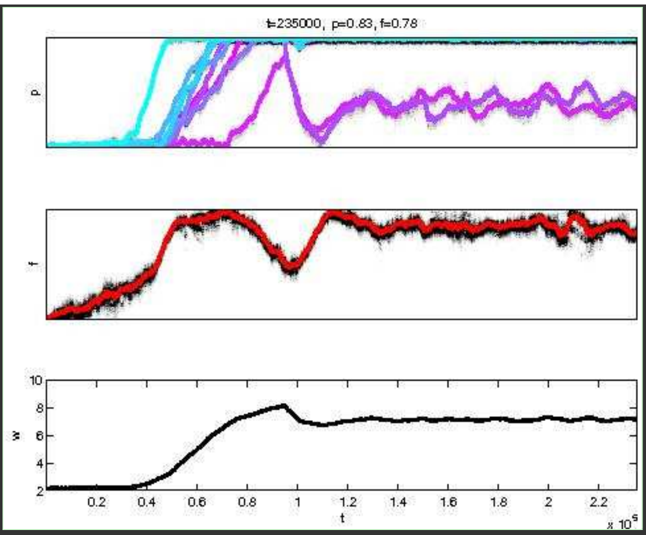

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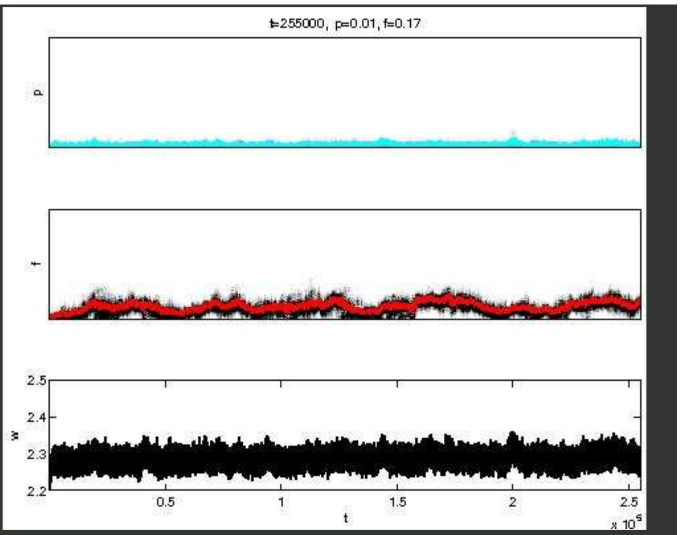

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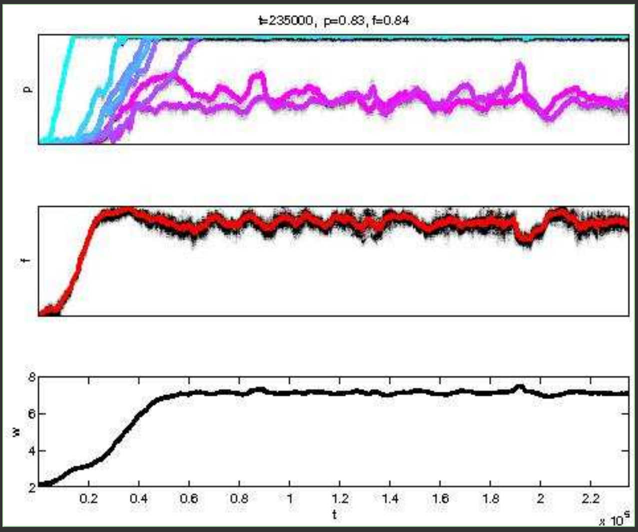

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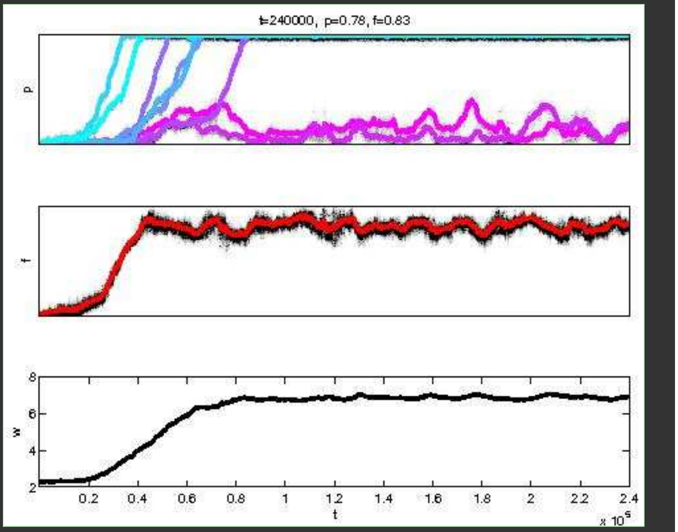

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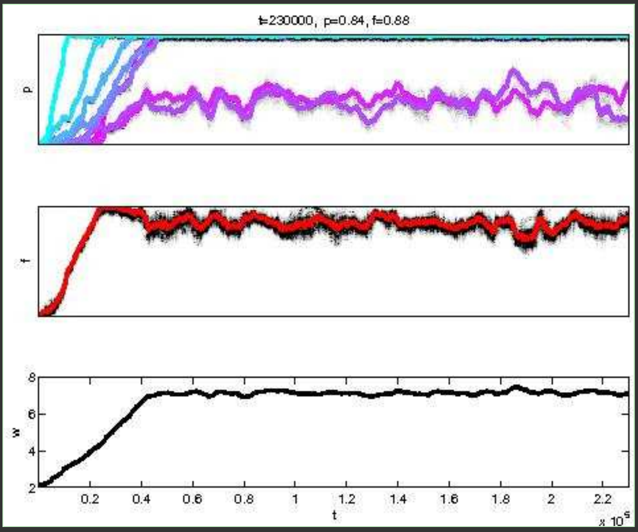

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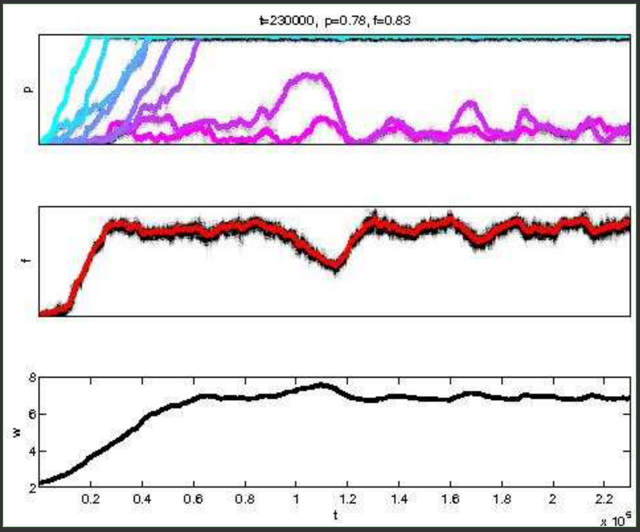

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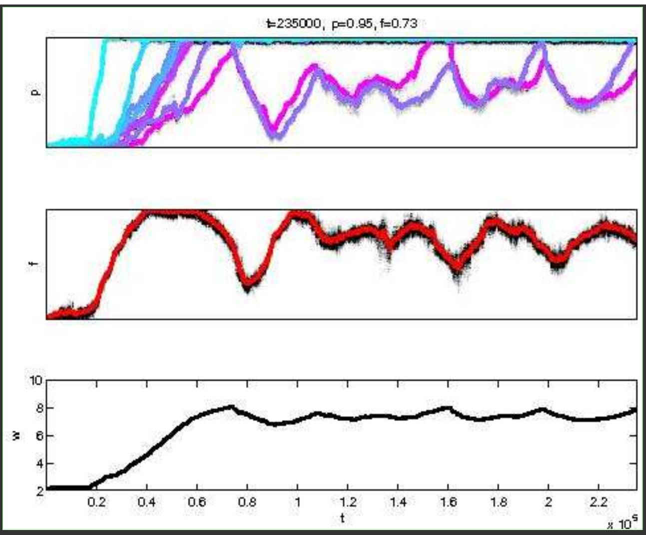

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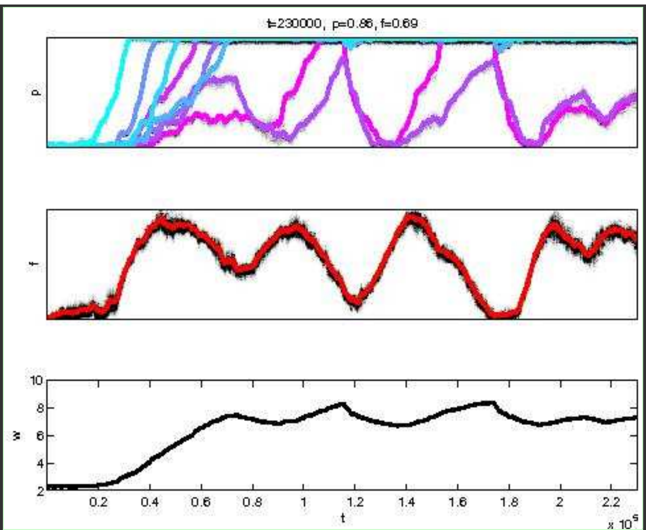

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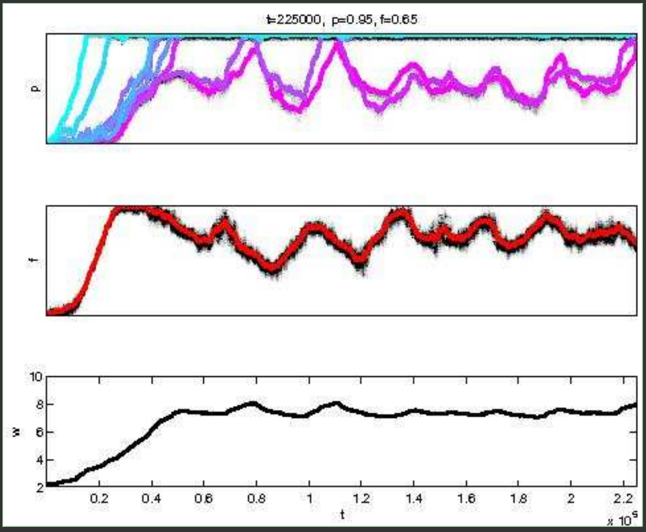

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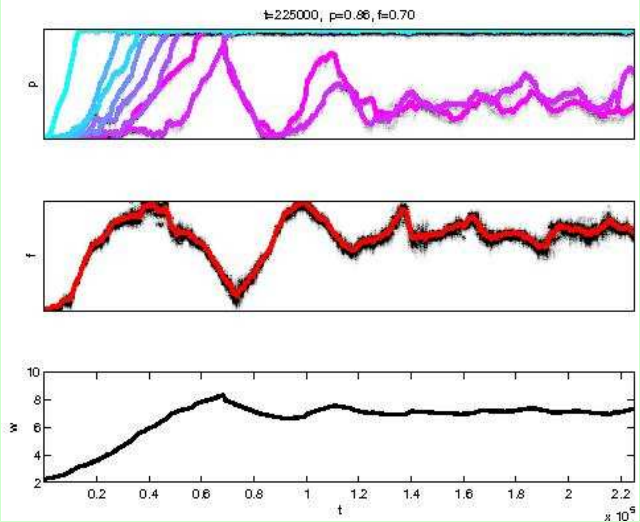

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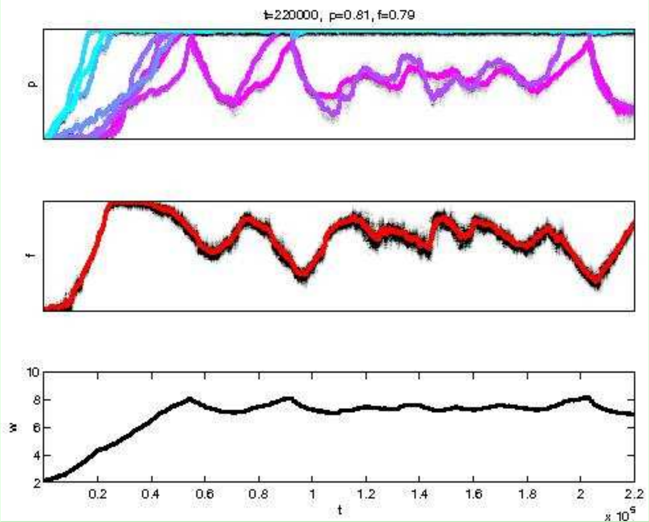

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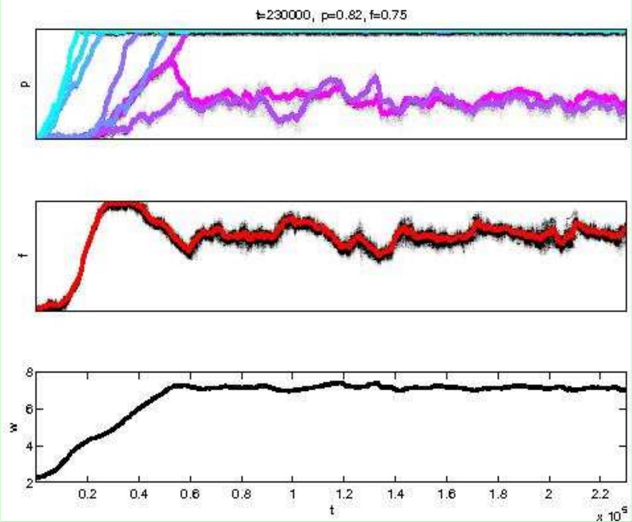

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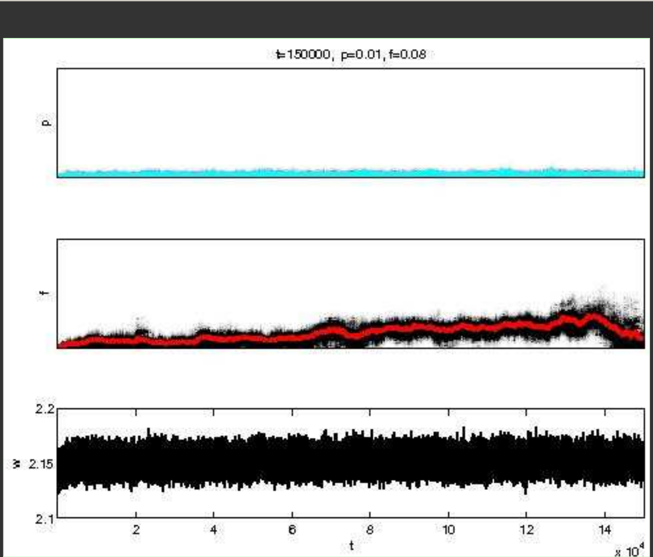
for /home/sergey/share/Mono/Newton/Long_runs/N16/

Number of images: 54
Created on: Thursday 30 June 2011



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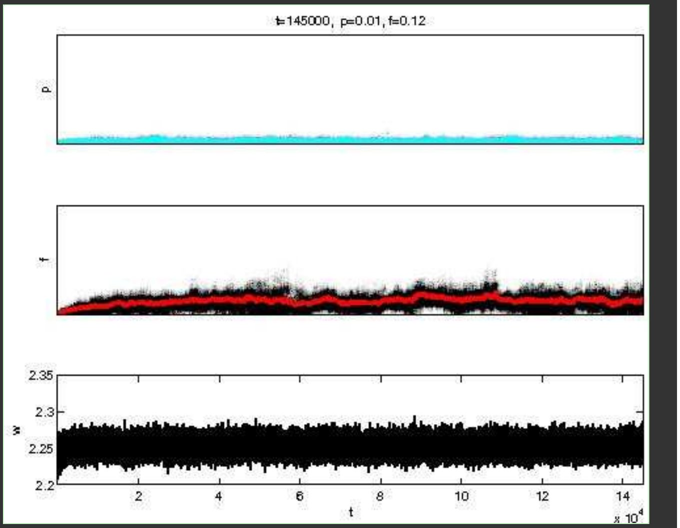

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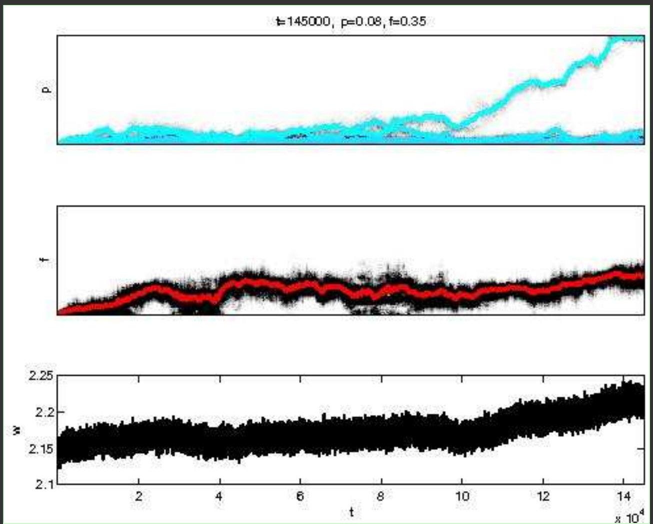

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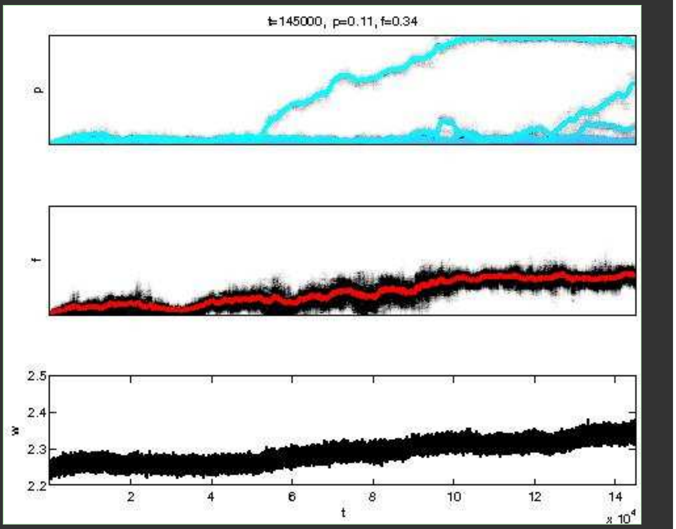

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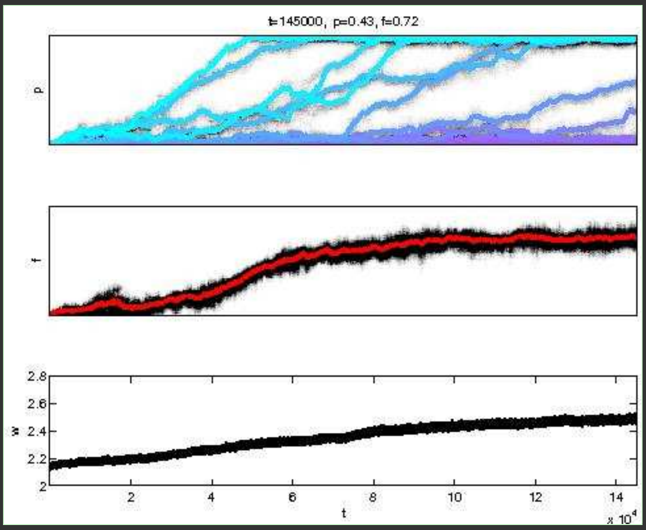

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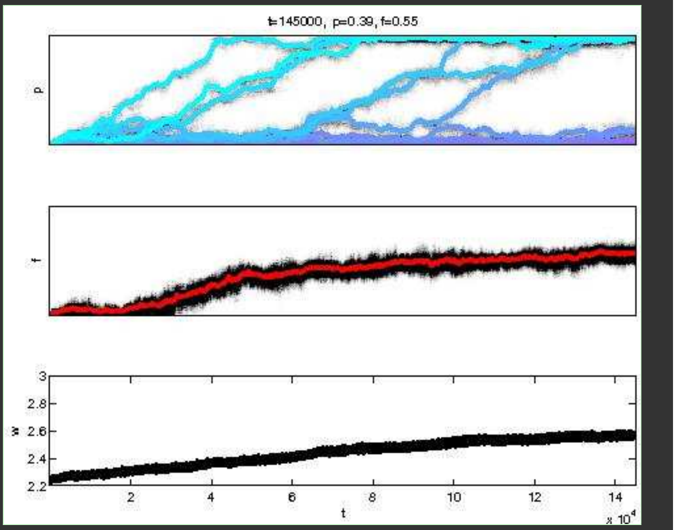

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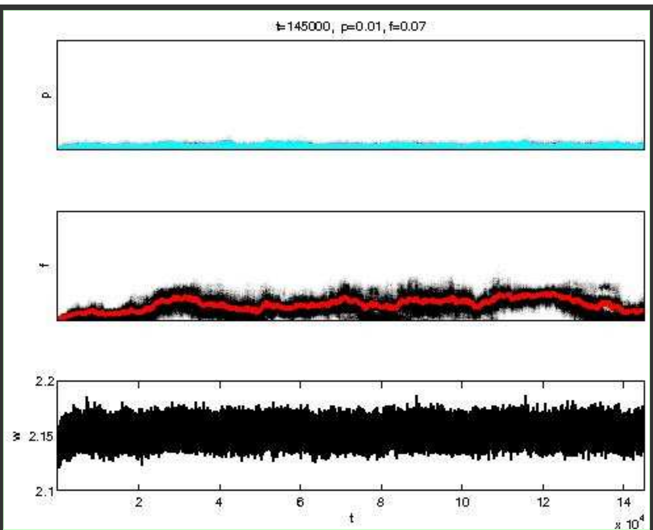

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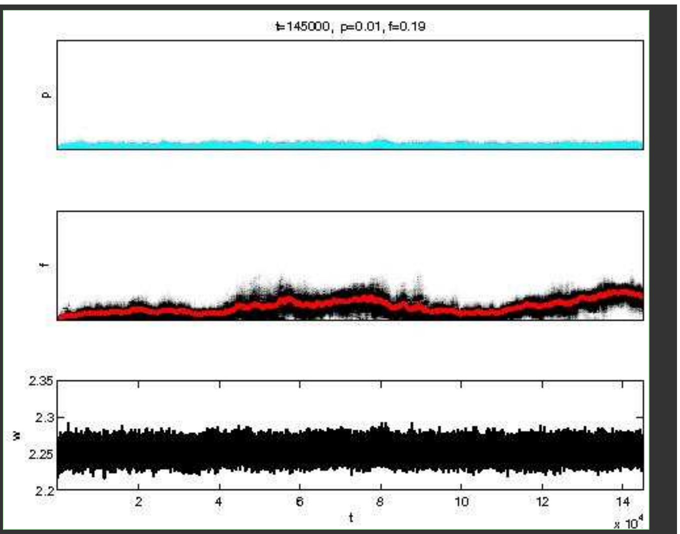

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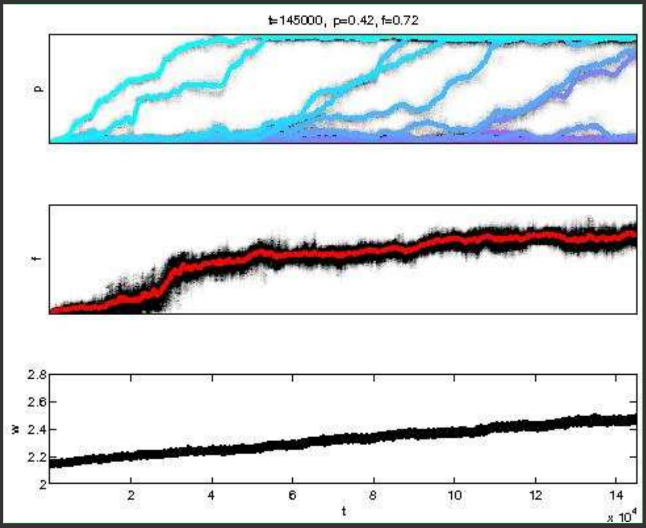

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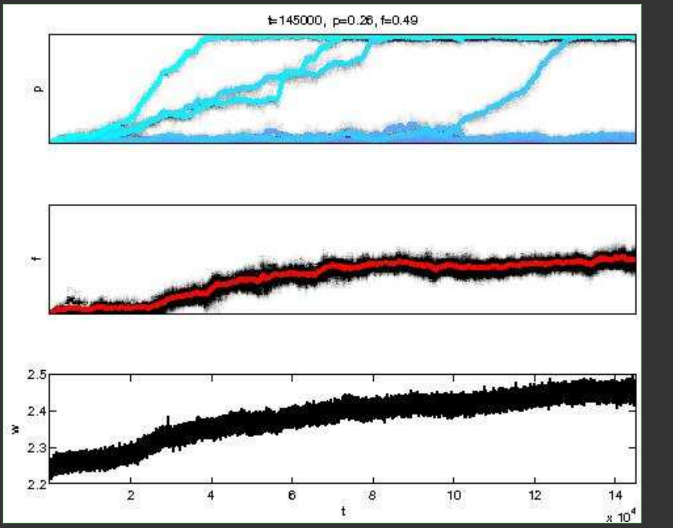

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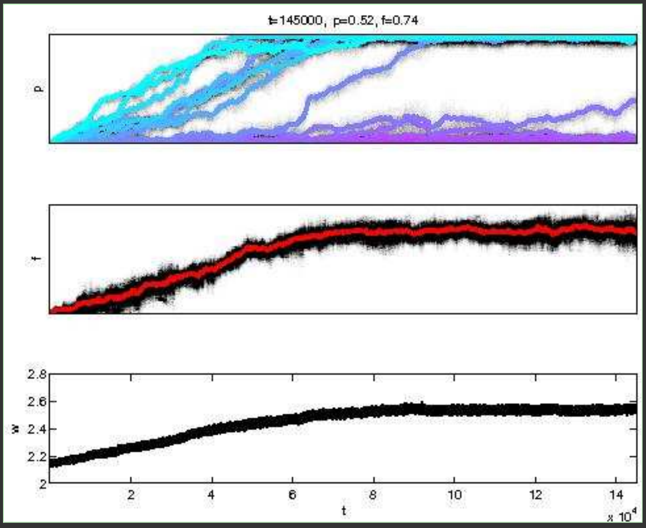

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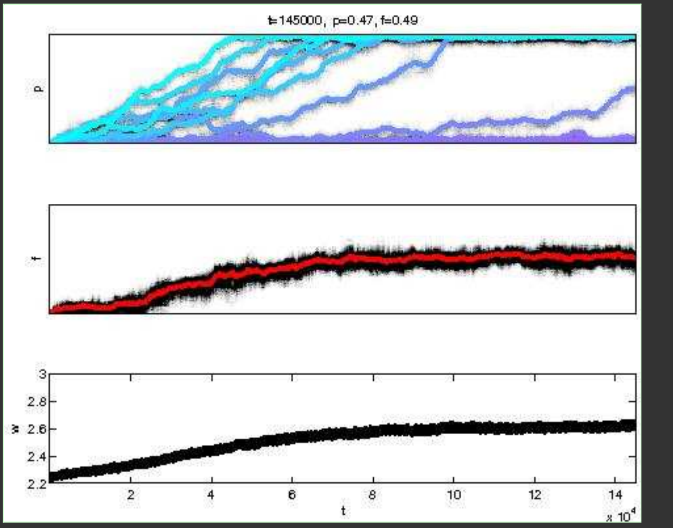

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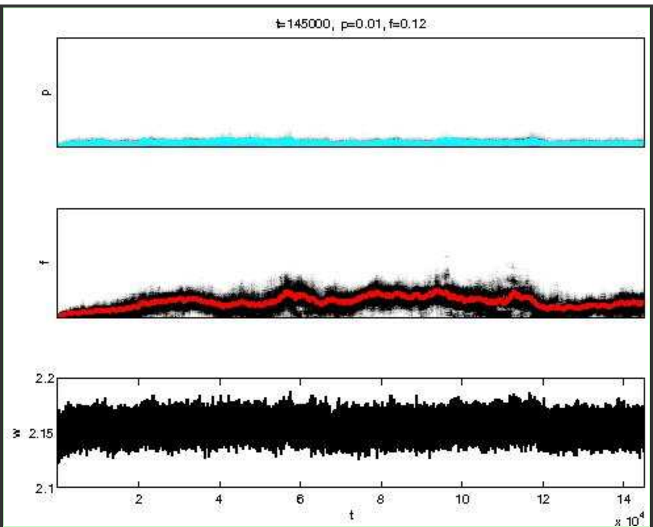

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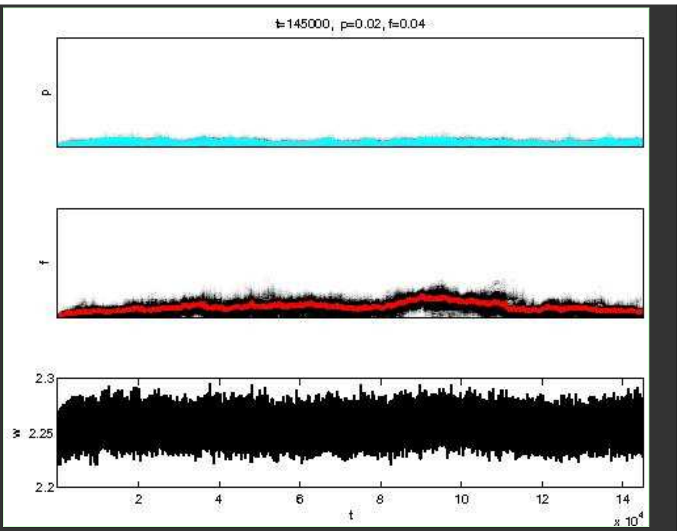

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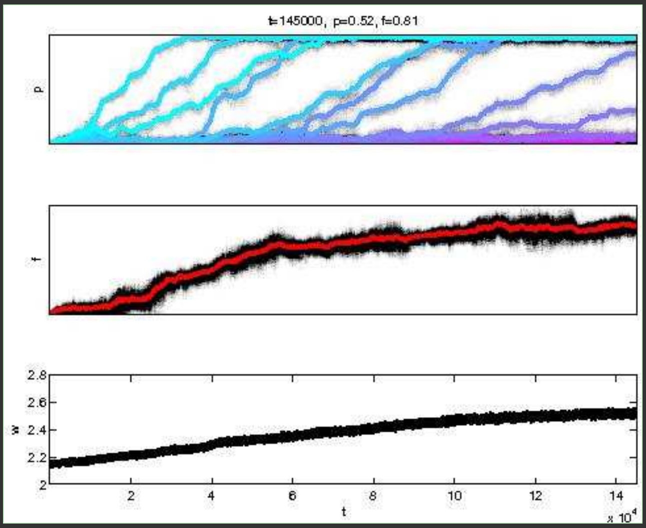

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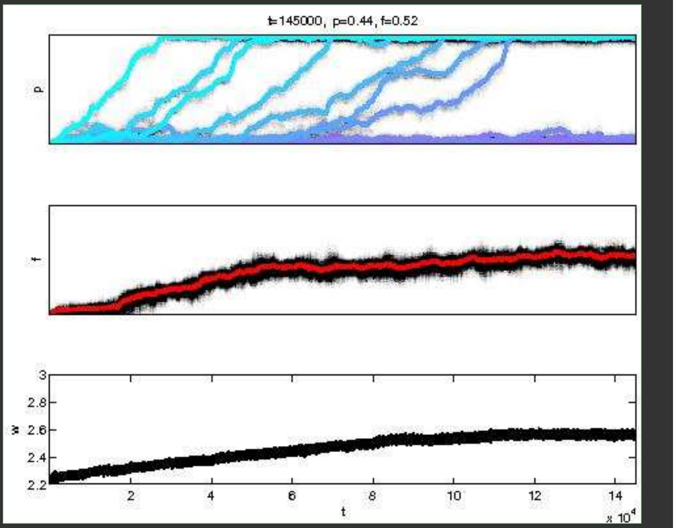

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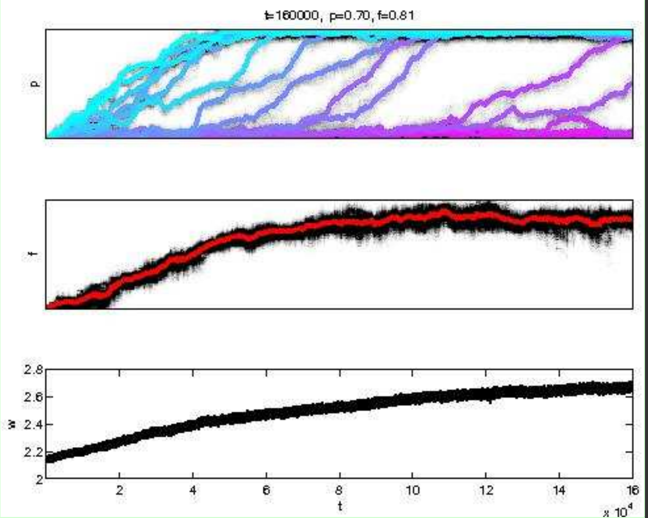

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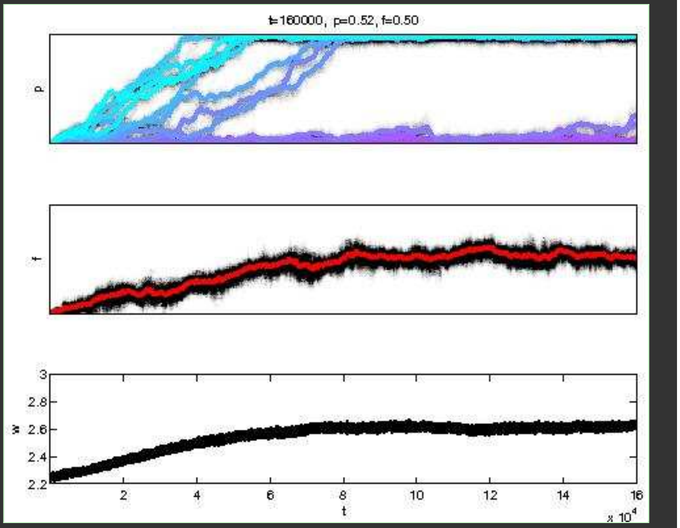

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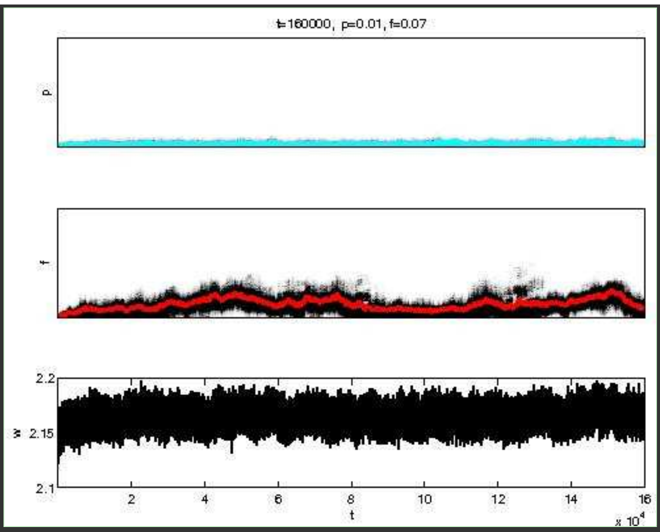

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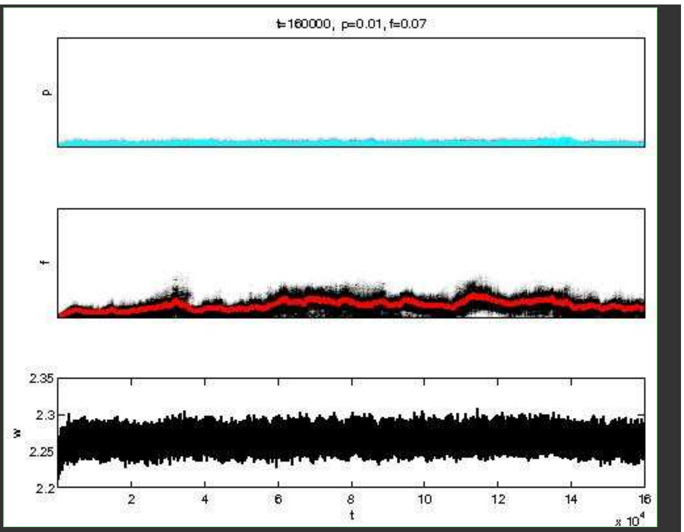

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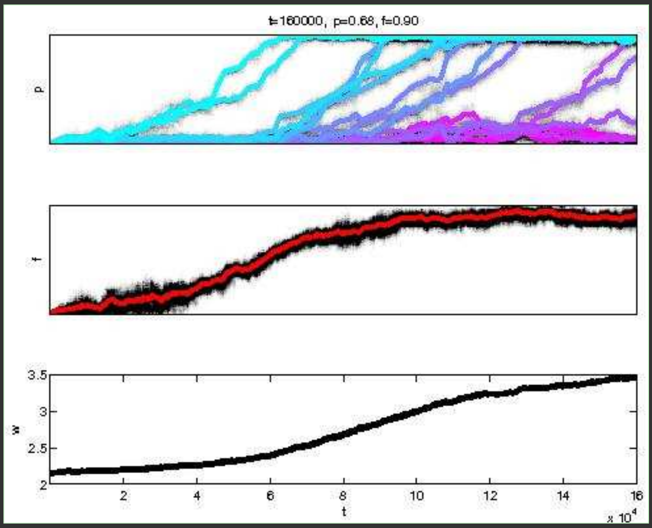

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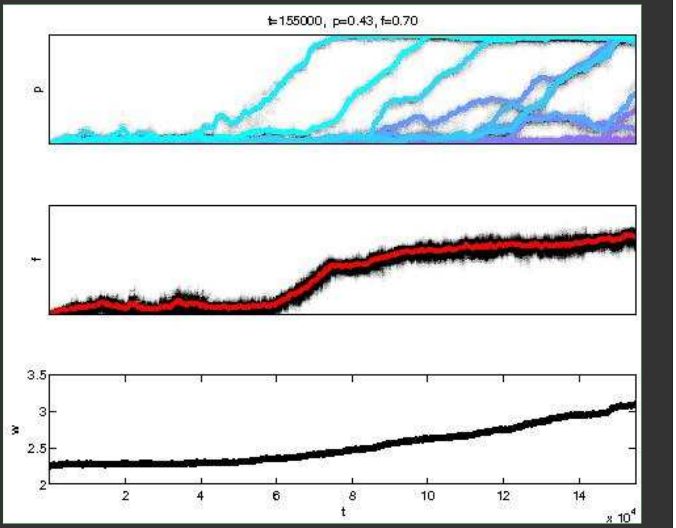

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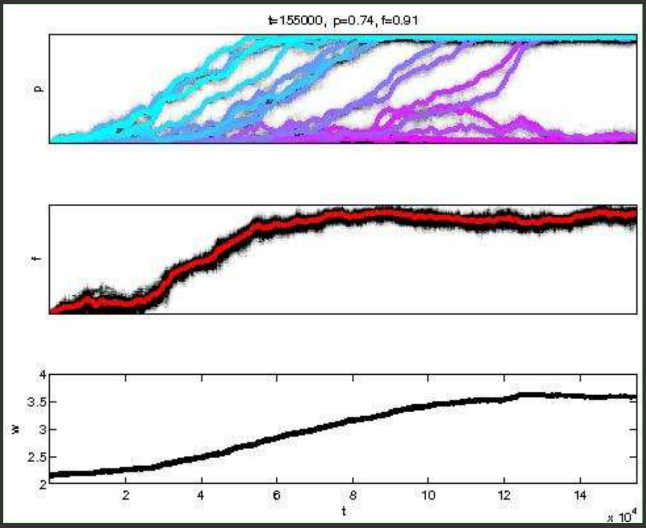

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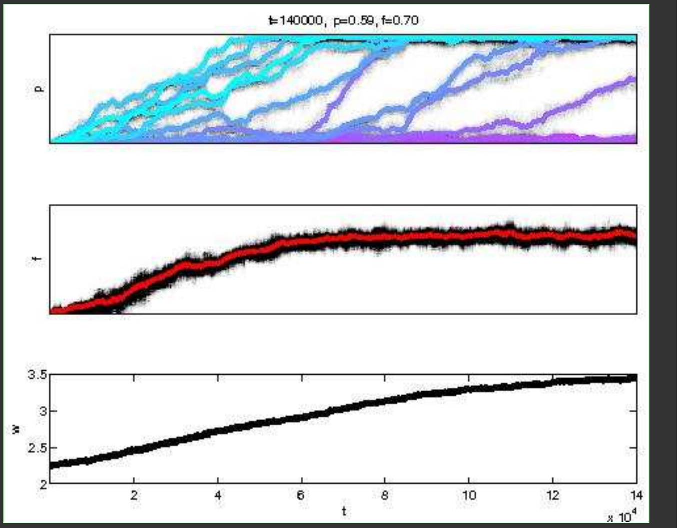

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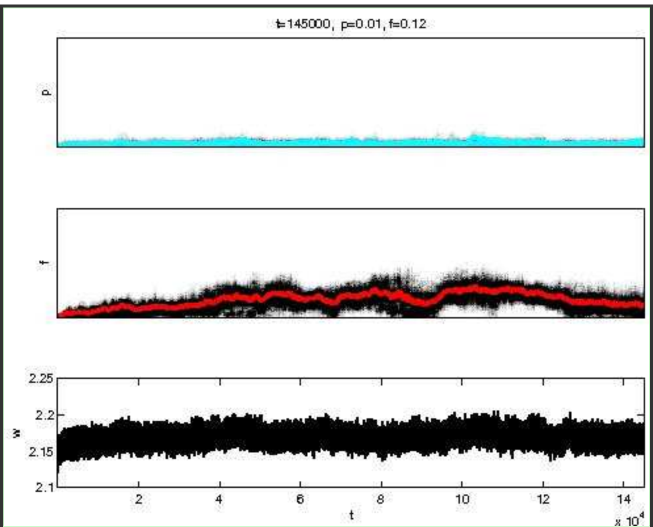

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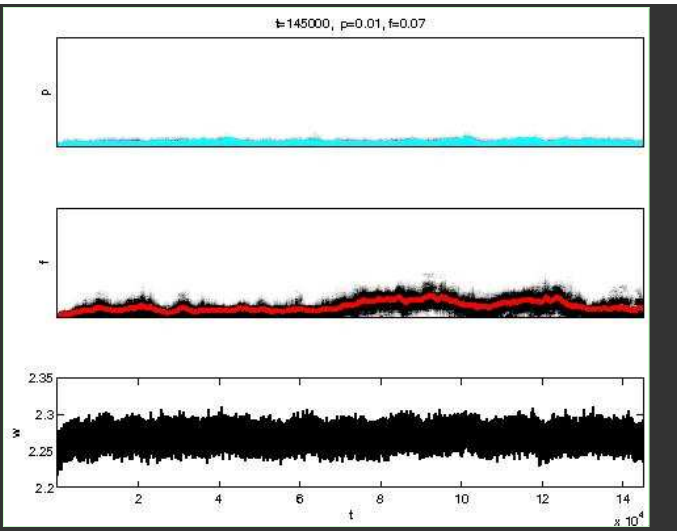

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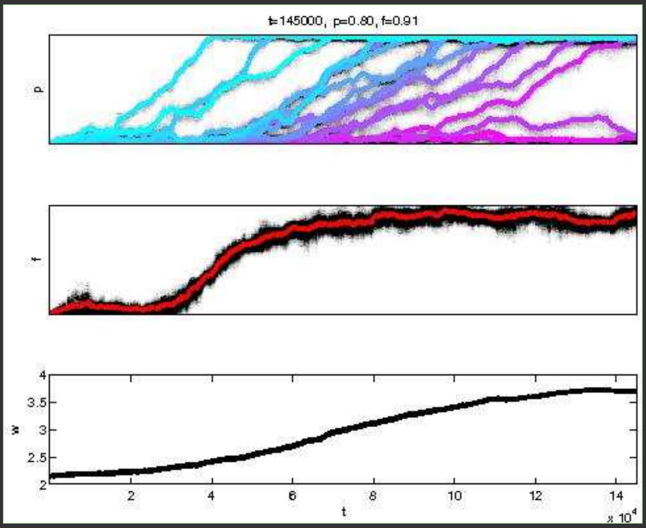

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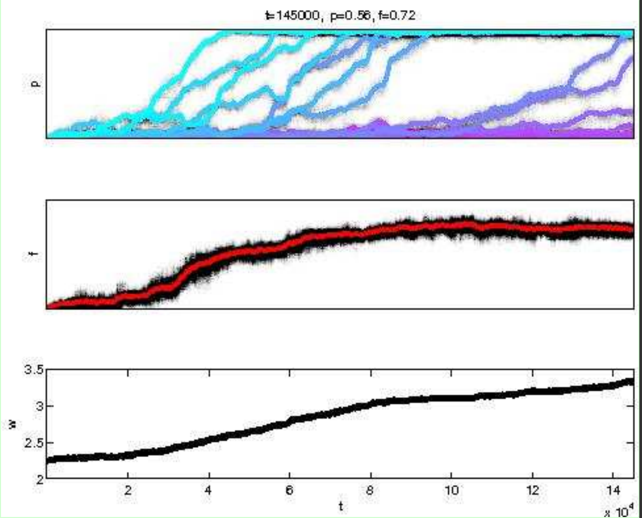

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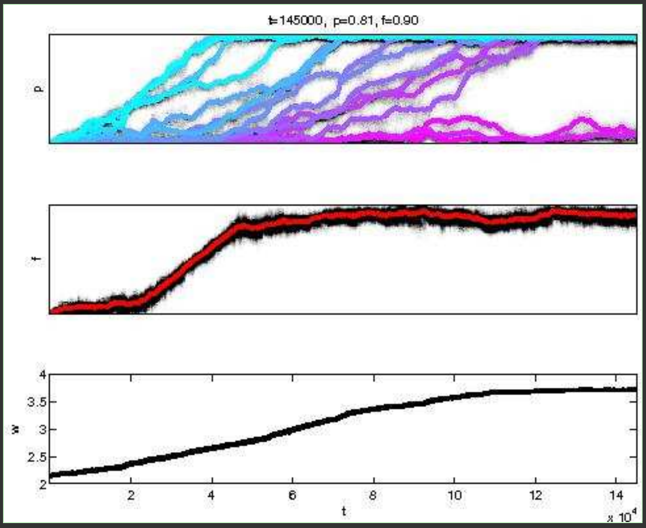

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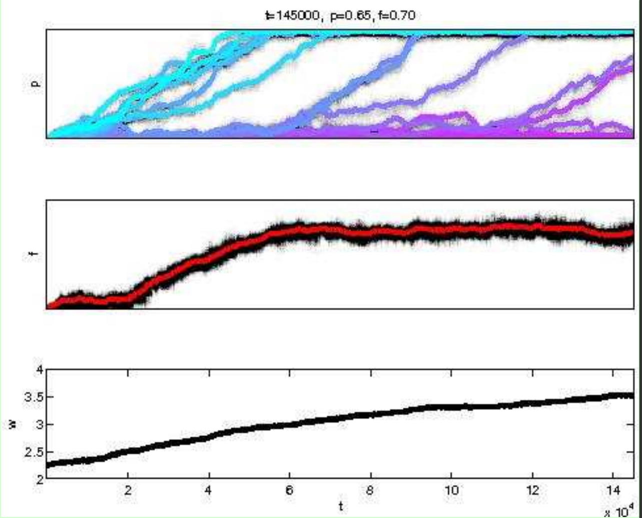

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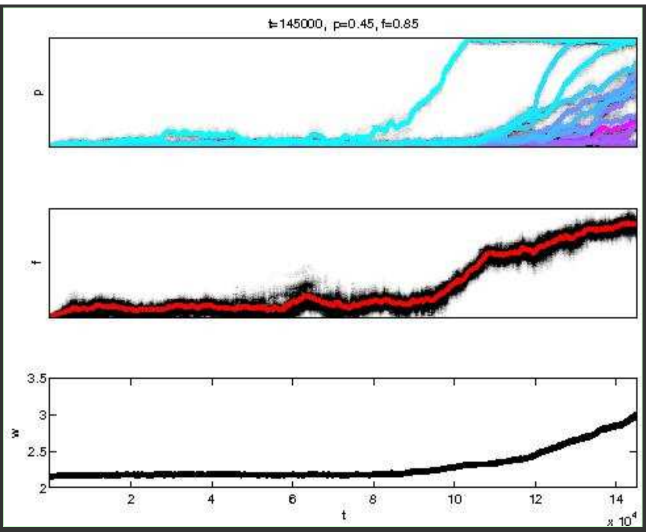

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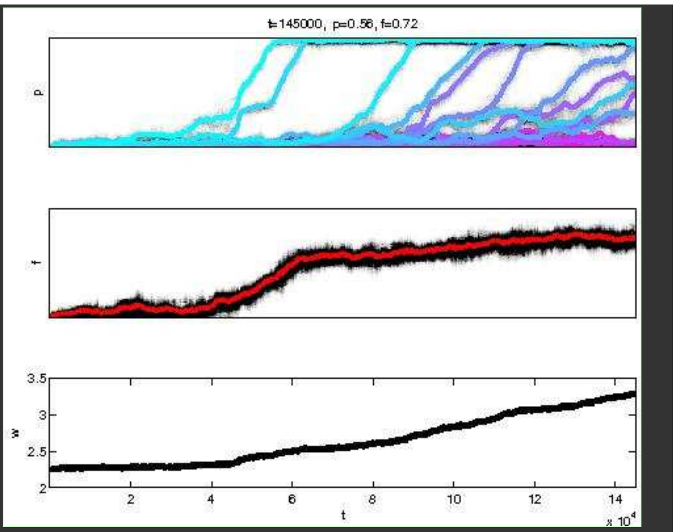

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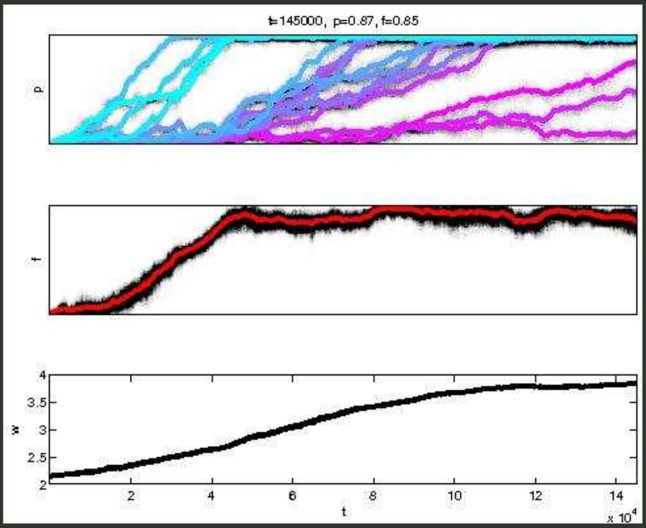

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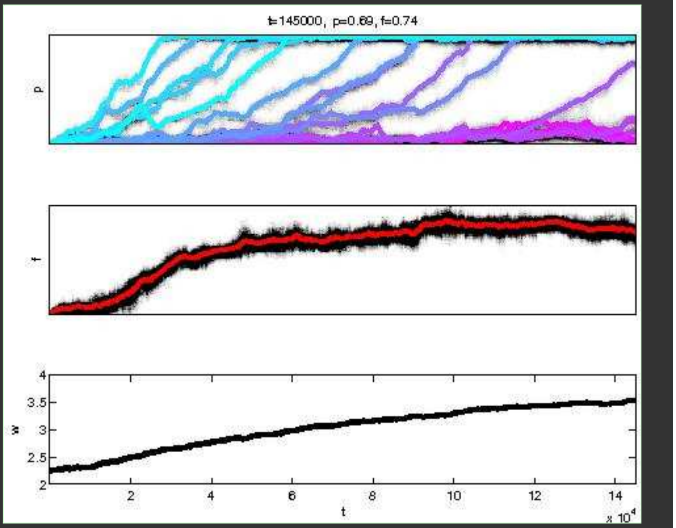

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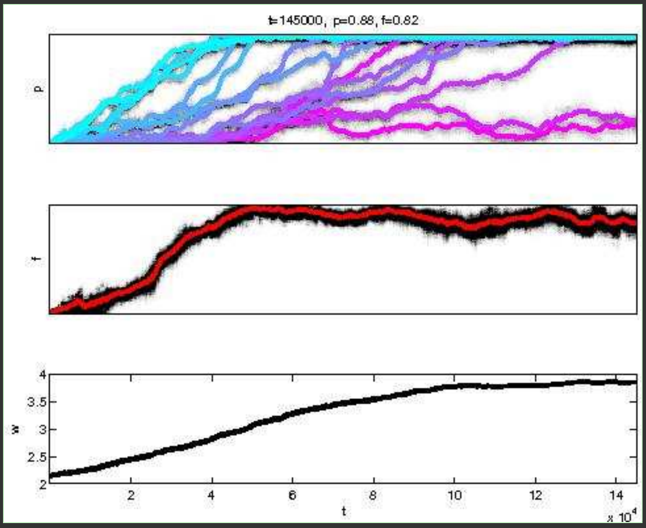

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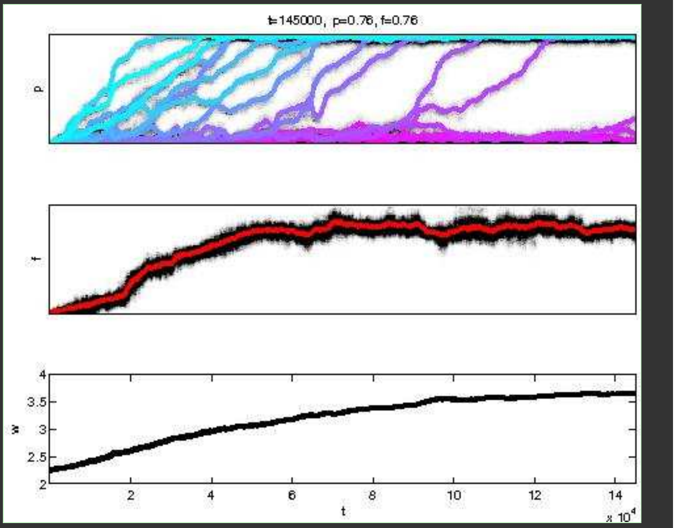

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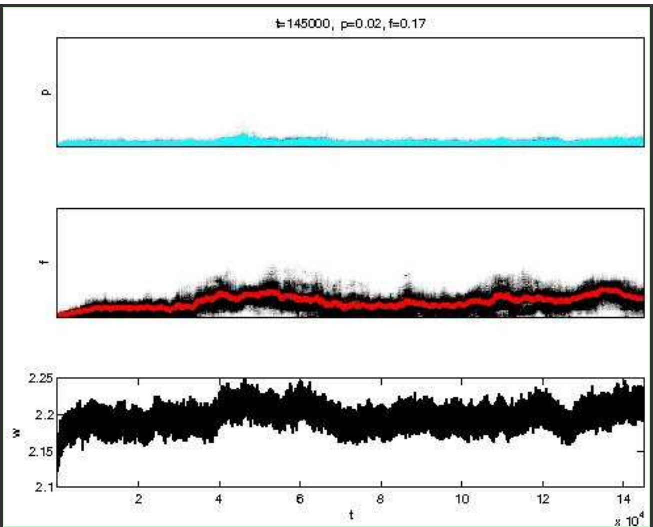

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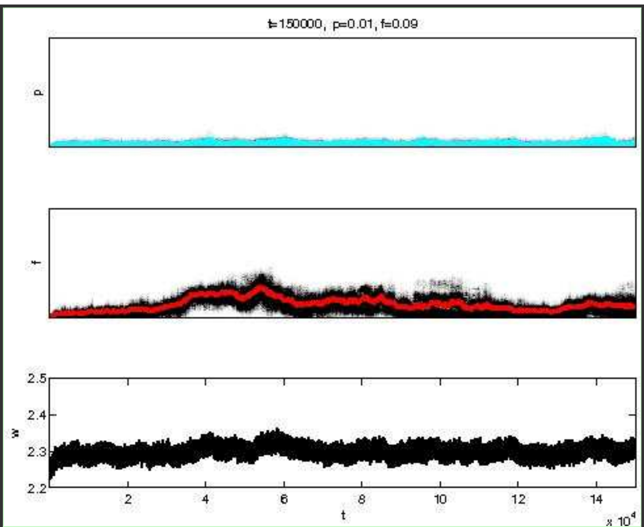

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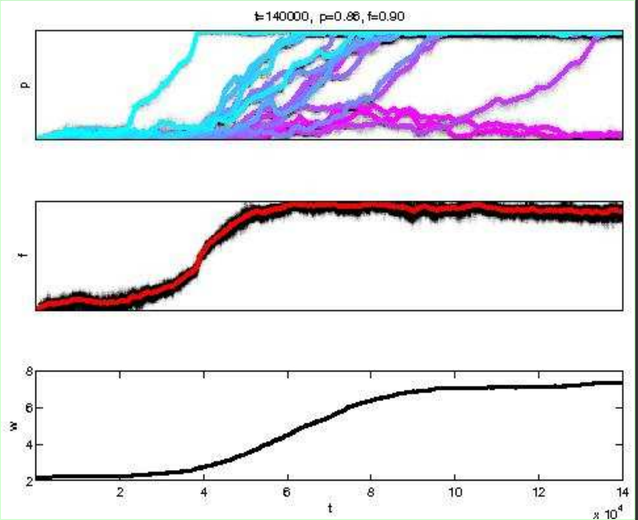

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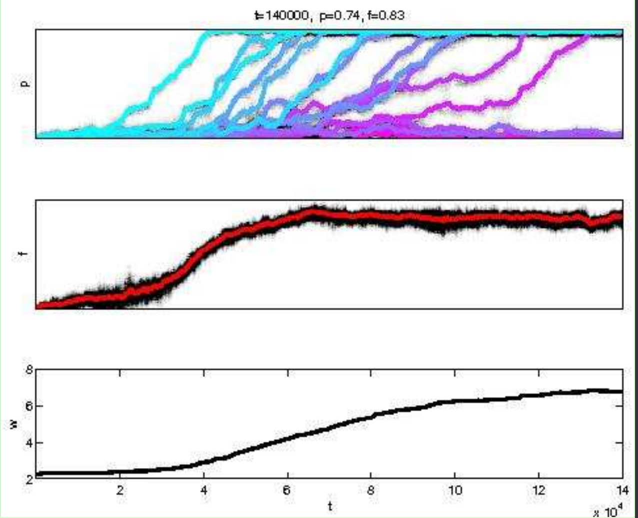

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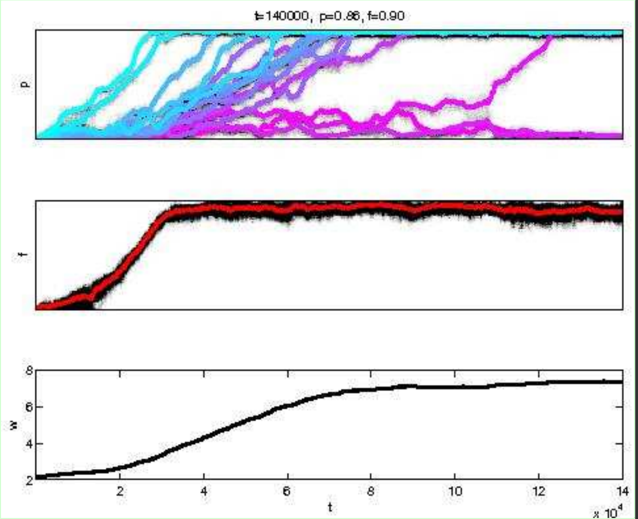

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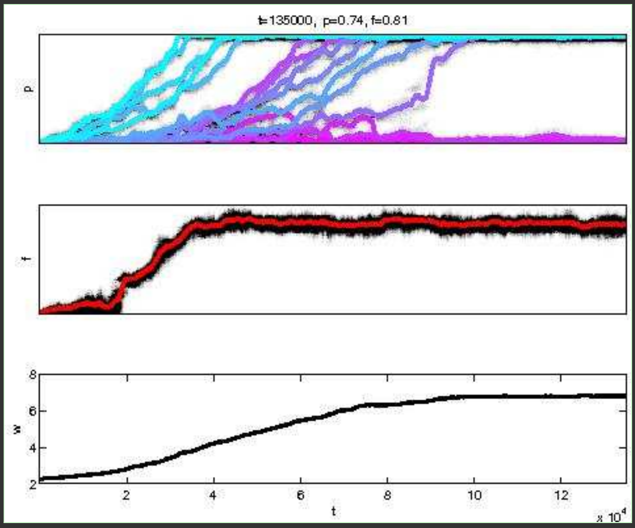

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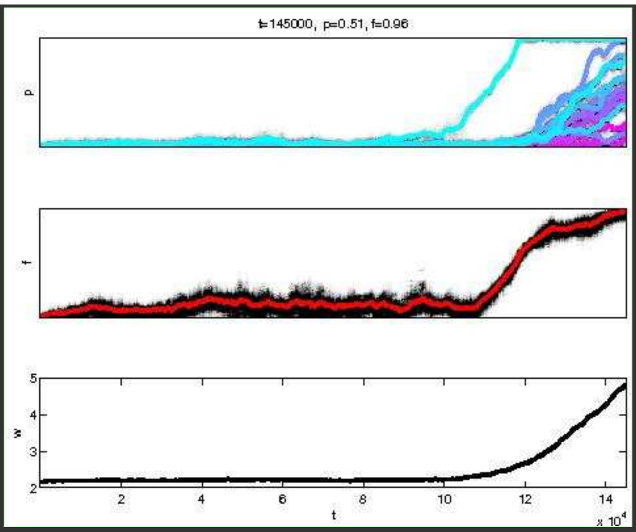

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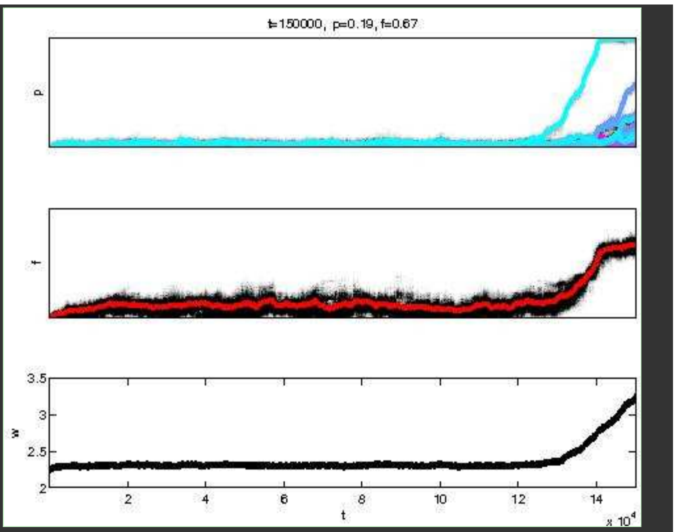

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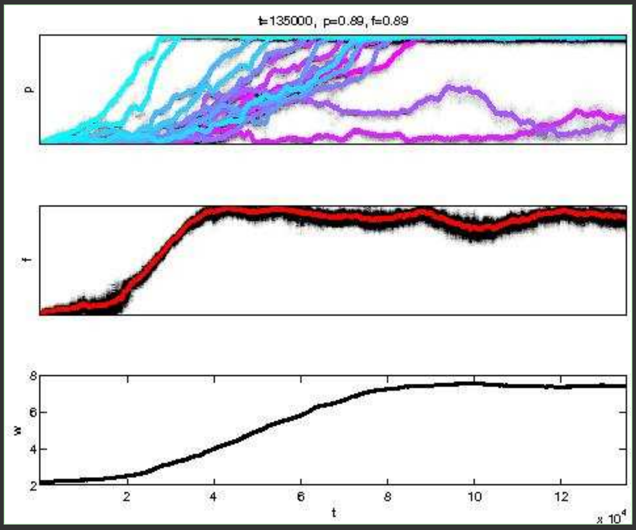

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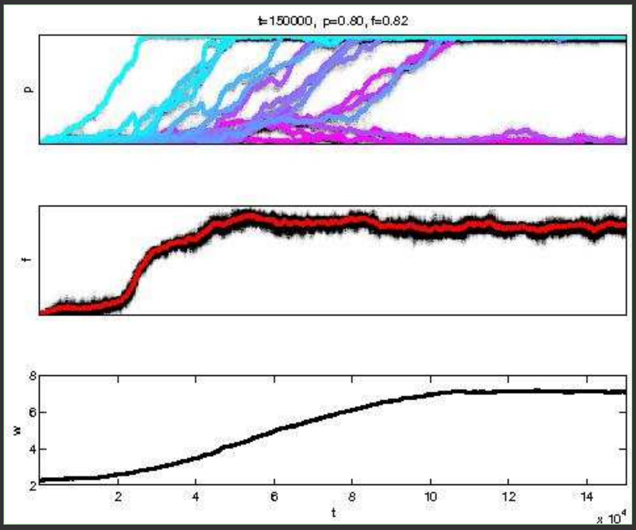

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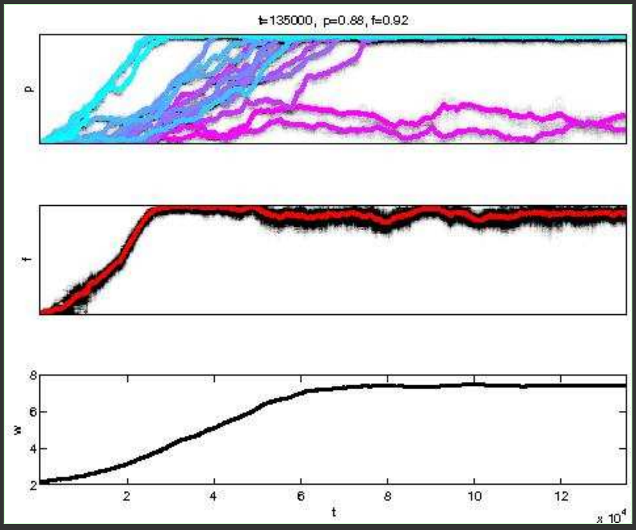

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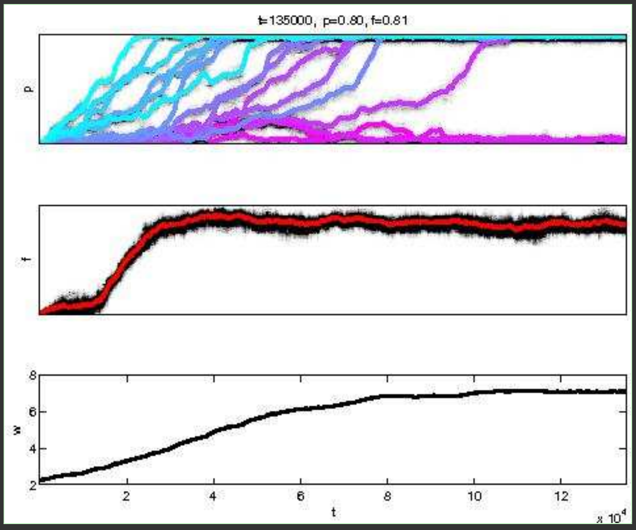

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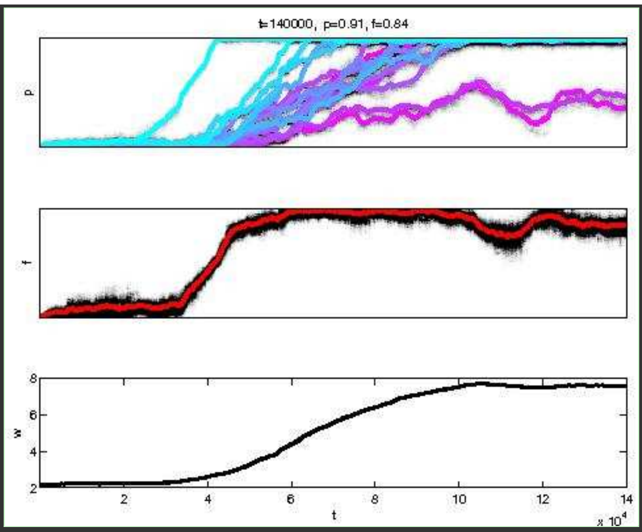

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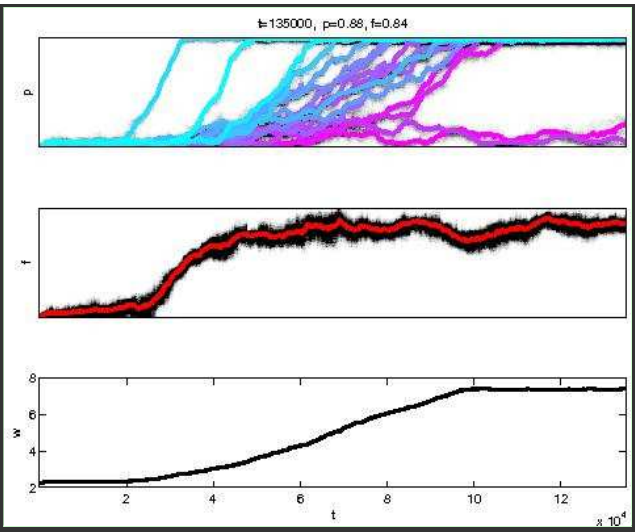

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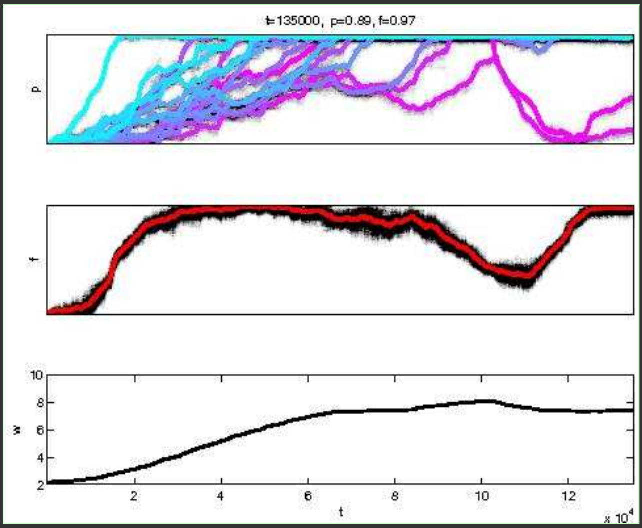

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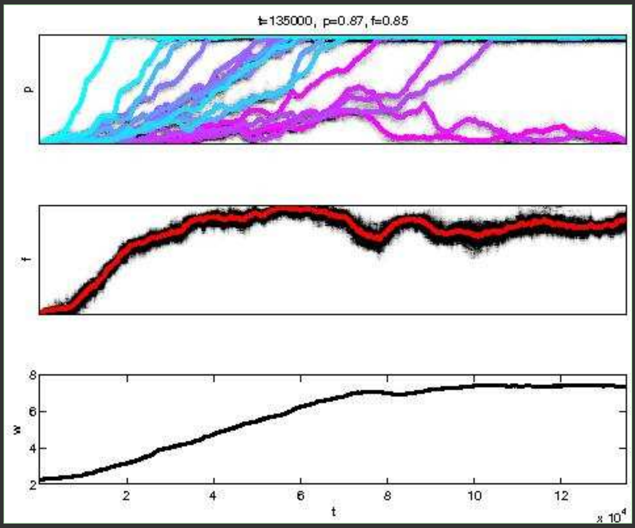

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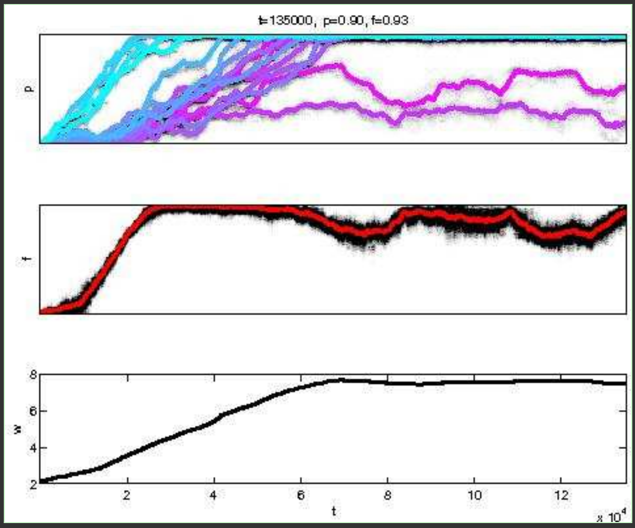

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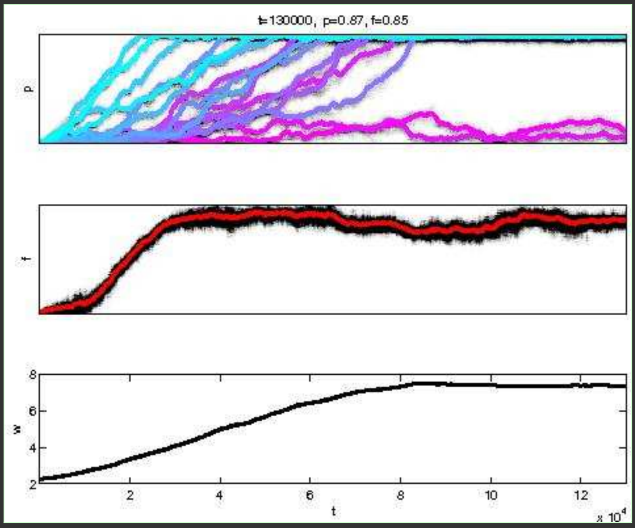

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