



The significance of sex

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ARTICLE INFO

Article history:

Received 25 July 2012

Received in revised form

14 September 2012

Accepted 17 September 2012

Keywords:

Entropy

Free energy

Natural process

Reproduction

The principle of least action

The two-fold cost of sex

ABSTRACT

Sexual and asexual modes of proliferation are associated with advantages and disadvantages, yet a profound percept that would account for both ways of reproduction is missing. On the basis of the 2nd law of thermodynamics we find that both sexual and asexual reproduction can be regarded as a means to consume free energy in least time. Parthenogenesis is a fast way to consume a rich repository of free energy, e.g., an ample stock of food with a large number of individuals, whereas sexual reproduction is a fast way to consume diverse and dispersed resources with a large variety of individuals. Most organisms have adapted to their surroundings accordingly and some organisms switch from one mode of reproduction to the other depending on the amount and dispersion of free-energy sources. We conclude that the least-time free energy consumption in respective surroundings, as the general criterion of natural selection, determines also sexual and asexual modes of reproduction.

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1. Introduction

For a long time it has been puzzling why some animals and plants reproduce sexually while others rely on asexual proliferation. On one hand a genetic recombination event will bring about more variation among a small population of individuals than a mere mutation within a clone (Fisher, 1930; Muller, 1932; Weismann, 1889). Already Darwin reasoned that siblings will be able to acquire more food from their environment than clones, because each distinct offspring may find and occupy a distinctive ecological niche (Darwin, 1889; Doncaster et al., 2000). Variation by sexual reproduction may also allow species to keep adapting to unrelenting environmental changes, e.g., to keep ahead in an arms race against parasites (Hamilton et al., 1990; Van Valen, 1973). Moreover, sexual reproduction seems to cause rivalries among individuals which can be seen as events of natural selection for the fittest (Darwin, 1859). Sex also promotes viable phenotypes by suppressing defunct genotypes (Kondrashov, 1988) and facilitating DNA repair (Bernstein et al., 1985).

On the other hand sex is also associated with costs, in particular with the two-fold cost of sex (Maynard Smith, 1978). Usually only one of the sexes, when excluding hermaphrodites, is capable

of bearing young. Thus, the other sexual partner appears obsolete after mating and even disadvantageous when depleting resources from its own offspring. Indeed in some spider species females can kill and eat males after mating. Furthermore, males and females must find each other to mate, which will invariably slow down reproduction. In contrast individuals of an asexual species are capable of giving birth on their own and are thereby able to generate a large population rapidly. Moreover, it is conceivable that sexual selection may also favor some traits, such as glorious feathers, which will reduce rather than increase survival of individuals when threatened by predators (Maynard Smith, 1978). If fitness were merely equated with proliferation, sexual reproduction is disadvantageous because it will pass only half of an antecedent's genes to offspring (Ridley, 1995). Thus, sexual reproduction would seem to conflict with the selfish-DNA hypothesis (Dawkins, 1976). Moreover, in some organisms sexual reproduction will enhance the spread of parasitic genetic elements (Hickey, 1982).

The origin of sexual reproduction is also uncertain. It may stem from an exchange of genetic material, i.e., horizontal gene transfer to which, e.g., also bacteria resort (Judson, 2002). Alternatively, it has been suggested that sexual reproduction came from selfish parasitic genetic elements as these elements spread with sex (Hickey, 1982). The common, although not ubiquitous two-sex convention may be linked to the double helical DNA structure of mutually complementary strands (Halvorson and Monroy, 1985). Specifically, genetic recombination seems to be a mechanism to suppress expression of de-functional genes.

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All in all the significance of sex has attracted many to propose meaningful mechanistic explanations, though not necessarily universal rationalizations of sex. In this study we will neither advocate for some specific scenarios from which sex could have originated nor propose some specialized mechanisms that could maintain sex, but we will seek for a more general selective principle of both sexual and asexual proliferation from the fundamental law of nature.

2. Aphids as an example organism

Remarkably, some species are able to adapt to their environment by choosing between sexual reproduction and parthenogenesis. The switch from one mode of proliferation to the other implies that there is, in given circumstances, a subtle balance between the two modes. In the following we will exemplify and analyze the ubiquitous motif that underlies a taken mode of reproduction.

Aphids, also known as plant lice or greenflies (blackflies or whiteflies in Britain and the Commonwealth) are the small green insects commonly found on plant leaves and stems. Aphids are among those species capable of both sexual and asexual reproduction (Grzimek, 1975; Wrensch and Ebbert, 1993). The simple annual lifecycle of Aphididae at temperate zones displays a clear and distinct switch between the two modes of proliferation. In the spring a larva will hatch from an over-wintered egg and develop into a wingless large female parent fundatrix. Its offspring are also wingless females, i.e., virgins exsulans that proliferate by parthenogenesis. During the summer these will produce several sequential virgin-generations, i.e., estivals that are clones. Usually virgins are vivipara, i.e., they give birth to live larvae. As the autumn arrives the last generation of summer females known as sexupara will have airborne progenies with both males and females, i.e., sexuals that cannot reproduce asexually. After mating the female sexual will lay only one or at most a few hard-shell eggs. Those eggs that winter will develop the next spring into new fundatrix, which will carry on the cycle of reproduction.

Conversely, the life cycle of aphids that have adapted to constant conditions and steady climates such as those prevailing in greenhouses, cellars and other protected places, just as in the tropics, display no bisexual phase. Obviously under steady-state conditions there is no need to survive winter as fertilized eggs.

The simple lifecycles of aphids both in varying and steady surroundings as well as their straightforward behavior, i.e., feeding continuously on an energy rich sap, makes the aphids a suitable species to analyze what is the significance of sex. Namely, we ask ourselves, what is the profound principle that determines the mode of reproduction?

3. The principle of least-time free energy consumption

Our analysis of reproduction is based on the universal law of nature, which is known by many names, most commonly as the principle of least action (Georgiev and Georgiev, 2002; Maupertuis, 1744), the 2nd law of thermodynamics (Carnot, 1824), the principle of increasing entropy. Also the maximum entropy production principle in its informational (Brooks and Wiley, 1988; Collier, 1986; Jaynes, 1957) and physical (Lorenz, 2002; Mahulikar and Harwig, 2004; Martyushev and Seleznev, 2006; Matsuno and Swenson, 1999; Salthe, 1993; Schneider and Kay, 1994; Ulanowicz and Hannon, 1987; Ziegler, 1983) meaning can be seen as expressions of the universal law. The law says that an energy difference of any kind, i.e., free energy will be consumed in the least time. The thermodynamic tenet is general, but we will keep exemplifying it in the context of aphids.

The energetic status of a system, such as an ecosystem, in its surroundings can be derived from statistical physics of open

systems (Annala and Salthe, 2010a; Kaila and Annala, 2008; Sharma and Annala, 2007). The logarithmic probability P measure is entropy

$$S = k_B \ln P = k_B \sum_j \ln P_j \approx k_B \sum_j N_j \left(1 + \sum_k \frac{A_{jk}}{k_B T} \right) \quad (1)$$

where the free energy $A_{jk} = \mu_k - \mu_j + i\Delta Q_{jk}$ contains energy differences of chemical potentials $\mu_j = k_B T \ln[N_j \exp(G_j/k_B T)]$ (Gibbs, 1993–1994) and energy in radiation ΔQ_{jk} that couple to the jk -reaction and k_B is Boltzmann's constant. The chemical potential denotes the energy that is bound in the population N_j , where each individual is associated with $G_j/k_B T$. It is a familiar concept of chemistry yet valid for all entities, when using the self-similar formalism that spans across levels of natural hierarchy (Annala and Kuismanen, 2009; Salthe, 1985). In other words, thermodynamics makes no demarcation between animate and inanimate mechanisms of free energy consumption (Annala and Annala, 2008). For example, the aphid population N_j is one among many populations of mechanisms that constitute the energy transduction system, commonly referred to as the food web. Likewise, the supplies of energy for the aphids, essentially sugar molecules in sap are numbered by N_k and valued by $G_k/k_B T$. Sugar, in turn, is produced by plants when consuming the energy difference denoted by $i\Delta Q_{jk}$ in insulation relative to the cold space. The notation using the imaginary part for dissipation just makes it explicit that the vector potential of radiation is orthogonal to the scalar chemical potentials that are bound in the diverse populations (Tuisku et al., 2009). In the ecosystem there are obviously many more species than the aforementioned, and the formalism in Eq. (1) will index them alike so that the conservation of quanta is satisfied.

When $\ln P$ in Eq. (1) is multiplied with the average energy of the system $k_B T$, the bound $k_B T \sum_j N_j$ and free $\sum_j N_j A_{jk}$ forms of energy become explicit. The approximation in Eq. (1), due to Stirling for indistinguishable combinations $\ln N_j! \approx N_j (\ln N_j - 1)$, implies that $k_B T$ is a sufficient statistics for the distribution of energy, i.e., $A_{jk}/k_B T \ll 1$. In other words, the energy content (heat capacity) of the system is big enough so that birth or death of a few individuals will not cause a marked change in the average energy of the system. So, changes in the ecosystem appear mostly continuous. However, when powerful mechanisms of energy transduction repeatedly devour resources faster than they can be replenished, the populations will oscillate (Belousov, 1958; Strogatz, 2000; Volterra, 1931). Even then the statistical approximation will hold for the entire ecosystem, but not for a specific population when it emigrates from surroundings, or is about to emerge from evolution or to go extinct (May, 1976). These critical events (Bak, 1996) are best characterized directly by dP_j/dt . The change in P will be abrupt at a phase transition or, e.g., at a brisk change of climate, when the system is forced rapidly to reorganize its entire energy transduction network.

The general and holistic formalism allows us to describe systems within systems when they evolve to attain a stationary state in the respective surrounding system. For example, the aphid population is a system in its ecosystem. When there is a difference between the substrate potential μ_k , e.g., sugar in sap and products μ_j , e.g., aphids, the free energy will be consumed by changes in sugar and aphid populations as well as in all other populations that interact with aphids and sugar in sap. The formalism allows us to denote all determinants of entropy as potentials and various pathways for synthesis and degradation of diverse populations to the precision of a single quantum. Obviously in practice it would be impossible to actually carry out such a precise bookkeeping, but it is conceptually important to realize that the formalism strictly complies with the conservation of quanta that underlies causality (Annala and Salthe, 2012a; Tuisku et al., 2009). If not, room will be left for uncertainty or unfounded reasoning about causes and effects.

Due to diverse natural processes the entropy of the system will increase at a rate

$$\frac{dS}{dt} = \frac{1}{T} \sum_{j,k} \frac{dN_j}{dt} A_{jk} \quad (2)$$

where the population change $dN_j/dt = \Sigma \sigma_{jk} A_{jk} / k_B T$ is proportional to the free energy. The proportionality coefficient, denoted by σ_{jk} , refers to the species specific mechanistic qualities to consume free energy, such as sexual or asexual reproduction mode (Annala and Salthe, 2010a; Kaila and Annala, 2008; Sharma and Annala, 2007). When there is a source of free energy, i.e., affinity $A_{jk} > 0$, indexed by k , for a given population N_j of species j , e.g., aphids, S will continue to increase by proliferation $dN_j/dt > 0$. The growth will consume A_{jk} , e.g., sap. Conversely, when $\Sigma A_{jk} < 0$, the particular population N_j has already exceeded its resources. Subsequently entropy will increase when the population declines one way or the other to re-attain balance with respect to its over-consumed surroundings. The diverse processes, growth just as decline, aim at bringing the ecosystem to a stationary state with respect to its surroundings. The system will tend to move toward more probable states along the least-time paths of entropy production, i.e., along the steepest gradients of free energy reduction. This quest is in accordance with Newton's 2nd law, $\mathbf{F} = d\mathbf{p}/dt = \Sigma A_j dN_j/dx = TdS/dx$ which says that momentum of the system will change, e.g., by proliferation, to follow the net force which sums up the gradients in energy.

The equation for the entropy increase (Eq. (2)) can be analyzed to see that for a given transduction mechanism the initial growth will be exponential as if the resources were unlimited. When the resources begin to diminish, the growth will turn to follow a power law. Eventually when the resources are exhausted, the growth will decay exponentially (Grönholm and Annala, 2007; Mäkelä and Annala, 2010). The overall shape of the growth curve is of a familiar sigmoid, which is on a log–log plot mostly a straight line. Also evolution in its entirety will be punctuated from a stationary state to a rapid change by new mechanisms of free energy consumption, and eventually the natural process will level off to another stasis (Annala and Salthe, 2010a; Eldredge and Gould, 1972). This ubiquitous sigmoid character of natural processes is also apparent in ecological succession (Würtz and Annala, 2010).

The mathematical analysis of Eq. (2) will also reveal that distributions of populations are skewed, nearly log-normal distributions whose cumulative curves mostly follow a power law (Barabási and Albert, 1999; Kleiber, 1932; Pareto, 1906; Schroeder, 1991; Limpert et al., 2001; Würtz and Annala, 2008). Also in the context of sex, it is relevant to note that it follows from thermodynamics that the spread of a distribution, such as a population of gas molecules and a mixture of chemical compounds increases with its increasing average energy of the system. From this perspective, the sexual reproduction that is frequently found as the mode of reproduction among individuals of relatively small populations at the top of a food web, is seen here according to the thermodynamic tenet as a means to generate ample variation in a comparatively small population.

4. Application of the law on aphid proliferation

We will illustrate the principle of least-time free energy consumption (Eq. (2)) first for the aphids and then discuss the general principle in a wider context. When the spring arrives, the source potential $\Sigma \mu_k$ will increase, i.e., sap will become available for the aphid population N_j to proliferate. When the affinity $A_j > 0$ is high, the rate of entropy production is limited by dN_j/dt that denotes the aphid's reproduction rate. Presumably the rate is constrained by various factors such as molecular mechanisms, cellular functions as well as by behavior at the level of the organism, however

these mechanistic details are only at service of free energy consumption, not in command of the natural process. Under these very favorable conditions parthenogenesis as a faster and simpler method of proliferation will be preferred over the more involved and slower sexual reproduction. The rate of asexual reproduction that has perfected itself over eons for the least-time consumption of free energy, manifests itself also in the way virgins give birth to live larvae rather than laying eggs to hatch later.

The aphid clone will initially grow exponentially because the resources of free energy appear unlimited, but subsequently during the summer the growth will turn to follow a power law and eventually during the autumn the growth will begin to level off and ultimately asymptotically when $\mu_j(t)$ of aphid population closes in to equal the substrate potential of sap $\Sigma \mu_k(t)$. During the early summer when leaves are still growing, the early phase may last long since also the supplies $\Sigma \mu_k(t)$ will continue to increase, but eventually the source potential will begin to level off as the leaves mature and perhaps even decline as plants start to suffer from the aphids.

The switch from the asexual to sexual mode will take place as the autumn approaches. When photosynthesis slows down, the available free energy $A_j(t)$ for aphids will decline invariably. Then the rate dN_j/dt is no longer the bottleneck of entropy production, but dS/dt is curtailed by the free energy terms A_{jk} . Then the sexual reproduction will contribute to dS/dt more than the asexual mode by resorting to variation that resulted from selection in the past, allowing airborne sexuals to access diminishing supplies, and more importantly to find a variety of potential wintering grounds at least for some eggs to survive the coming harsh season.

When the winter arrives, the conditions of entropy production will change dramatically so that $A_j(t)$ will turn negative and aphids will die in great numbers. It is up to the vital functional mechanisms that are deposited in the variety of fertilized eggs deposited in diverse places to resist degradation during the harsh period without the external energy supply. When the spring arrives anew, those eggs that hatch will revive entropy production using the replenished source potential $\Sigma \mu_k$.

Admittedly, the description of aphid life cycle using general thermodynamic terms may appear overly technical or as if it were ignoring important details. Yet, the value of the formalism of physics given by mathematical formula is in its generality and accuracy. Despite being concise in notation, the equations denote every quantum. Therefore it is possible to analyze unambiguously the switching point from asexual to sexual reproduction. It is given by the condition $(dS/dN_a)/(dN_a/dt) < \Sigma (dS/dN_{vj})/(dN_{vj}/dt)$, where dN_a/dt denotes the asexual reproduction rate of a clone and dN_{vj}/dt the corresponding sexual production rate of a variant j . The condition means that the aphids will switch from asexual to sexual reproduction when the source potential $\Sigma \mu_k$, which is available for aphids by their means of energy transduction, becomes the limiting factor of free energy consumption. Then to ensure a higher entropy production in future conditions, the sexual reproduction will be selected to generate a greater variety in the relatively small population of fertilized eggs than to continue the cloning which will yield ever smaller variation by mutations in the decreasing population. The non-linear response to the changing conditions is also apparent from the logarithm form of μ_j . Undoubtedly the switching mechanism from one mode of reproduction to the other has refined itself during evolution and become embedded in numerous functions that orchestrate reproduction with an annual rhythm.

5. Discussion

The association of the rate of entropy production with the fitness criterion of natural selection is not a new notion (Bejan and Marden,

2009; Chaisson, 2001; Lineweaver, 2005; Matsuno and Swenson, 1999; Salthe, 1993; Schneider and Kay, 1994; Whitfield, 2007). However, when it is given in a mathematical form of the equation of motion, it can be analyzed to draw unambiguous conclusions (Annala and Salthe, 2010a; Sharma and Annala, 2007). The general formalism can be used to analyze a variety of phenomena without disciplinary demarcation. The disciplinary characteristics of natural processes, such as proliferation, stem primarily from mechanisms that are typical of a specific system or a particular process. When the general concepts of physics are used, the operational principle of nature can be expressed independently from systemic characteristics and process properties. The accurate account, however, does not imply determinism. Accordingly no precise predictions can be made for a given setting, because the ensuing natural motion, such as proliferation, and its driving forces, such as food supplies, cannot be separated from each other to solve the evolutionary equation of motion. This inherent intractability was regarded already early on as a deficiency of the principle, yet, it is in fact the characteristic of evolution (Annala and Salthe, 2012b).

When the modes of reproduction are regarded as mechanisms of entropy production, the switching between asexual and sexual reproduction as well as between sexes by hormonal secretion even within a lifetime of an individual of some organisms can be comprehended consistently. Natural selection does not relate only to any specific mechanism such as gene expression, but the least-time free energy consumption is the general and comprehensive mode of operation that all natural processes will follow. For many species the repositories of free energy will provide an unambiguous bias either in favor of sexual or asexual reproduction. The particular mode is subsequently maintained and perfected during evolution so that it has become an integral part of the species. Even if the species were later exposed to circumstances in which the established mode of proliferation were no longer optimal, it would take a long time, i.e., a lot of free energy (Tuisku et al., 2009) for the species to readapt its mechanisms of reproduction for optimal performance in the new settings.

It is no coincidence that higher organisms with longer lifetimes tend to reproduce sexually and lower organisms with shorter lifetimes asexually. Higher organisms have many functions to consume free energy and therefore these species will benefit from the powerful and refined mechanisms of free energy consumption that stem from sexually produced variation in their comparatively small populations. Practically all higher taxa are sexual. High mobility of higher organisms is also a particularly viable function that favors sexual reproduction. When supplies are scant and far apart, recombination of genetic material may yield new essential mechanisms to search for new possibilities of entropy production, i.e., ecological niches. Sexual reproduction warrants higher organisms with greater variation of functions to struggle for survival, i.e., continue free energy consumption. For example, promiscuity is one way to enhance variation within a population that has passed through a genetic bottleneck (Michalczyk et al., 2011). Moreover, according to thermodynamics the spread of a distribution, e.g., when given in terms of kinetic energy, increases with increasing average energy of the system. The same trend of increasing diversity with increasing overall energetic status of a system can also be recognized in modes of behavior (Anttila and Annala, 2011) as well as in economic (Annala and Salthe, 2009) and cultural patterns (Annala and Salthe, 2010b).

Conversely, the asexually proliferating species tend to be at low levels in food chains, i.e., in networks of energy transduction. The lower organisms can display comparatively few functions in their bodies to consume supplies of free energy. A small animal or plant is simply limited in its functions and capacity to consume free energy hence the small organism cannot do much but accept and quickly make the most out of current conditions. When its surroundings

turn rich in energy, the fast asexual proliferation will rapidly produce a large population that will be able to harvest most energy. Conversely when surroundings turn poor in energy, the losses of comparatively inexpensive machinery of free energy consumption will not be all that dramatic.

It is illuminating that sawflies, hymenopterans that are more sophisticated than aphids, prefer sexual reproduction but resort eventually to parthenogenesis if no mate is found. The asexual mode is a secondary option for them since the offspring of a virgin is less fit to find its own way of living among clones due to the limited variation in comparison with variation among sexually produced offspring (Williams, 1975). Also a bee colony displays intricate methods of optimizing energy efficiency by producing drones asexually and eliminating them after mating with a queen.

In the same sense most plants primarily prefer not only sexual reproduction but also use their roots for asexual reproduction. Sexual reproduction is tied to the annual rhythm but rapid vegetative growth is an effective means to claim intact resources even within the season. Aspen's aggressive colonization of burned areas is a familiar example of asexual reproduction as a means to access quickly abundant resources that have suddenly become available.

The imperative of least-time free energy consumption sheds light on the two-fold cost of sex. Even when only the rate of reproduction is considered as the incentive of life, sex is associated with cost. Certainly also lots of free energy is consumed during mating and related activities such as courting and fighting. However, when the least-time consumption of free energy is taken as the imperative, then the costs of sex will be balanced as much as two distinct sexes can contribute to the entropy increase by their distinct yet co-operative functions. For example, many animal species display substantial differences between male and female behavior to optimize the overall usage of available resources. Also in general, there must be a difference from which to benefit whereas those alike have no natural synergy.

The resolution of the two-fold cost of sex by the least-time free energy consumption also explains why hermaphrodites are not more common than they are. In the thermodynamic sense individuals of a synchronous hermaphrodite, such as earthworms, belong to the same class as they are similar in their functionalities. Thereby they do not complement each other by sex-linked functions when extracting free energy from their surroundings. However, bisexuality is motivated when the additional cost of maintaining simultaneous male and female sex organs of hermaphrodites is outweighed by associated ability to consume free energy. Rapid reproduction coupled with large variation allows hermaphrodites to consume surrounding supplies that have appeared quickly or are abundant but may go off soon. Accordingly, animal hermaphrodites are usually protected from self-fertilization.

Sequential hermaphrodites, such as certain fish, will change their sex from male to female (protandry) or vice versa (protogyny). Likewise, some plants are consecutively monoecious and dioecious. In thermodynamic terms the switch from one mode to the other becomes motivated when $(dS/dN_m)/(dN_m/dt) < \Sigma(dS/dN_f)/(dN_f/dt)$, where N_m denotes the male population and N_f the female population. Obviously our reasoning based on the least-time free energy consumption is not that different from the argument of maximizing the reproductive success (Ghiselin, 1969) but it is more profound and general.

The general principle of least-time free energy consumption serves to analyze other sexually related systemic characteristics, e.g., to rationalize ratios of males to females. Furthermore, the least-time entropy production principle gives reasons why males of some species are equipped with minimal properties, practically capable of only fertilizing bodily females who will care for

the progeny and who will even consume the male when it has become obsolete. Moreover, the same universal principle clarifies why some other species invest so much energy in males. Namely, it depends on particular conditions whether the investment in muscular males is warranted by support and security provided by them for the entire community. For example, aggressive males might just be what will be needed for a population to claim rich grounds and thereby to acquire access to consume free energy in great quantities.

The physical portrayal of nature in a form of equation of motion would undoubtedly prompt one to compute outcomes and to make predictions. However, to include everything to the precision of one quantum of action would not only present a formidable computational task, but also it turns out that the evolutionary equation (Eq. (2)) cannot be solved. Technically speaking it is non-computable. When motions as flows of energy and their deriving forces as differences in energy cannot be separated from each other, natural processes are path-dependent. Consequently the evolutionary trajectories are intractable (Annala and Salthe, 2012b) and the character of nature is capricious (Keto and Annala, 2012).

In summary, our conclusions based on the least-time free energy consumption do not differ all that much from current hypotheses (Dawson, 1995) that asexual reproduction is favored when rapid population growth is important or in stable environments, whereas sexual reproduction generates genetic diversity to adapt to changing environments. However, the thermodynamic tenet emphasizes that reproduction is not an end in itself but its modes are dictated by the profound principle of nature. Since conditions for the free energy consumption are various and varying, so is the scope of sex wide and versatile.

Acknowledgments

We thank Dr. Keith Baverstock and Robert Leigh for their critical comments.

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