The trade-off between ageing and reproduction in the context of life histories

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Abstract

Ageing and reproduction are life history traits. In order to reach maximal fitness, the optimal reproductive strategy is necessary. Because ageing results in a decline in fertility, ageing is likely to affect late age reproduction. This article discusses the nature of the trade-off between the process of ageing and early age reproduction, and factors that cause this trade-off to occur.

Several theories explain the evolution of ageing and their link with reproduction. With extrinsic mortality being the main cause of death, organisms that are more susceptible to extrinsic hazards will be selected for early maturation. According to the mutation accumulation theory, the absence of purifying selection will result in a higher rate of ageing due to an accumulation of deleterious mutations having their effects late in life. The disposable soma theory suggests a direct trade-off between reproduction and ageing, through the allocation of resources. Energy that is invested in reproduction cannot be invested in somatic repair and maintenance and can lead to a faster rate of ageing. However the acquisition of resources can increase the rate of ageing as well, due to oxidative damage to cells.

There appears to be a dynamic trade-off between reproduction and ageing, with environment and the organisms' susceptibility to extrinsic hazards, the allocation and acquisition of resources being the main determinants in the trade-off.

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Introduction

According to the evolutionary theory, the purpose in any organism's life is to pass on its genetic information by reproduction to maximize its fitness. Each species has its own optimal reproduction strategy and variation between species can be large.

For example the Pacific salmon will build its life around reproduction and, after being born in fresh water and maturing in salt water; it swims upstream to lay its many eggs in fresh water, and will subsequently die within a few weeks after spawning. An elephant is much slower in reaching a mature enough age to reproduce, and when it does it gives birth after 22 months of gestation, to only one large calf.

Organisms have many different reproduction systems, all with the goal to maximize reproductive output. To be able to reach a maximal fitness, one would need to produce as many offspring as possible. However, individuals in nature will always have limited resources and investment in every aspect of life is simply not possible (Zafon, 2003). It is therefore impossible to create a Darwinian demon, an organism which has optimized all the aspects of life that affect fitness, at the same time.

Besides reproduction, another important aspect of life is the process of ageing. Ageing is a very common feature found in eukaryotes (Bell, 1988; finch, 1990 in Zwaan 1999), and it is a well studied yet complex process which can be explained by both molecular and evolutionary theories.

When considering life histories and looking from an evolutionary point of view, there appears to be a trade-off between reproduction and ageing (Kirkwood, 2000). Considering the importance of a high fitness, it is interesting to find out: What is the nature of the trade-off between the processes of ageing and reproduction in the context of life histories?

Chapter 1: The evolution of ageing

Before we explore the driving factors behind the trade-off between the process of ageing and reproduction in the context of life histories, it is important to define the concept of ageing. The process of ageing can be defined as "the total effect of intrinsic changes in an organism that adversely affect its vitality and functions and that renders it more susceptible to the many factors that can cause death" (Zwaan, 1999).
Ageing has a disadvantageous character because it causes the decline in reproductive performance and probability of survival with age (Partridge & Barton, 1993). Because of this there is a paradox in the evolution of ageing. This paradox is caused by the fact that, although natural selection is expected to optimize an individual's traits, the disadvantageous fitness and survival declining effects of ageing have demonstrated to have a genetic basis and to undergo evolutionary change (Partridge & Gems, 2006).
Even though there are alleles that have been identified to be able to accelerate the process of ageing, there are no genes known that have evolved specifically for ageing and the process is thought to have evolved as a side-effect of other causes of evolutionary change (Partridge & Gems, 2006; Partridge & Gems, 2002).

When looking at ageing from an evolutionary point of view, an important factor in the evolution of ageing is the dynamic between intrinsic and extrinsic mortality. Extrinsic mortality is caused by external factors such as predation, disease and accidents. The intrinsic mortality is caused by the effects of ageing, which is mainly a decline in body and tissue function. Adaptive evolution is driven by natural selection, which acts on the surviving reproductive output. Because fertility and survival decrease during the course of a lifespan, it is likely that the force of natural selection will decrease at the point when reproductive output has declined because there is no change in fitness after that point where natural selection could act upon (Medawar, 1952; Williams, 1957; Hamilton, 1966, but see Zwaan, 1999). There are three major theories that can explain the evolution of ageing in the context of the absence of natural selection.

First, the mutation accumulation theory of Medawar (1952) suggests that mutations with late age-specific effects are subject to weaker selection than mutations with early age-specific effects. Mutations that affect survival and reproduction early in life will be selected against very rapidly because they will affect fitness directly, whereas mutations that have their effects late in life, after reproduction has occurred, will hardly face any force of selection because their effects do not affect fitness. This way there is an accumulation of deleterious mutations later in life that will only become visible when organisms are capable to escape extrinsic hazards that affect longevity, such as predation.

Second, the theory of Williams (1957) on antagonistic pleiotropy suggests that genes can have pleiotropic effects both early and late in life. Because the force of natural selection decreases with age (Medawar, 1952; Williams, 1957; Hamilton, 1966, but see Zwaan, 1999), genes that have beneficial effects early in life have a high chance of being selected for even though they might have negative effects later in life and will increase the rate of ageing. The rate of ageing is therefore a result of a trade-off between benefits early in life and the subsequent rate of ageing (Patridge & Gems, 2006).

The third theory explaining the evolution of ageing, is the disposable soma theory. The disposable soma theory (Kirkwood, 1977 but see Zafon, 2003; Drenos & Kirkwood, 2005) suggests a trade-off between somatic maintenance and reproduction. The outline of the disposable soma theory is basically the same as that of the antagonistic pleiotropy theory, but it varies in that there is a suggested mechanism for the antagonistic effect of the genes. In the disposable soma theory the pleiotropic genes are thought to be involved in an optimization of resource allocation between reproduction on the one hand and maintenance and repair of the soma on the other (Kirkwood & Holiday, 1979). A certain amount of cellular deterioration is inevitable, and it is necessary to invest in repair and maintenance mechanisms of non-zero costs. But because extrinsic mortality is the most common mortality in nature, and intrinsic mortality due to the effects of ageing is very rare, a very high investment in somatic maintenance would often be a waste. Too little investment in maintenance and repair however, would lead to a higher rate of ageing, resulting in a premature death and therefore a low fitness (Drenos & Kirkwood, 2005). Reproduction requires a high energy input as well. Because reproduction is the most important aspect in natural selection it is much more advantageous to invest in than repair (Kirkwood & Austad, 2000).

All three theories imply that organisms will be affected more by the intrinsic effects of ageing if the extrinsic mortality in adults is small and that faster ageing will evolve when extrinsic hazards are great. An example in which individuals have evolved delayed senescence as a consequence of reduced extrinsic hazards was shown by Austad (1993) in his research on mainland and insular Opossums. The insular population had a long history of reduced predation, hence extrinsic hazards, and consequently, island females showed a delayed senescence of survival probability (Figure 1), reproductive performance and connective tissue physiology.
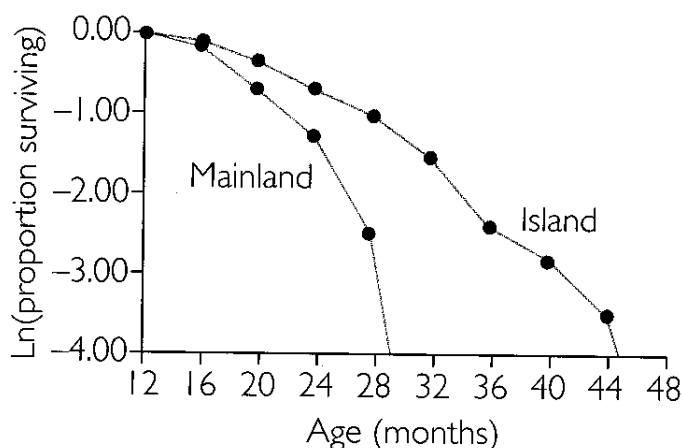

Figure 1: The rate of survival from one month to the next of female oposums. Females oposums of Sapelo Island age more slowly than those of the mainland (Stearns, 1992).

These theories indicate that longevity and ageing can be variable within lineages and even within a species depending on different environments with different extrinsic hazards. Because ageing results in a decline in fertility with age, and ageing is a variable trait, ageing is likely to affect reproduction. Because the life history theory is the main theory describing the effects of reproduction and ageing in populations, it is key to get a good insight in this theory.

Chapter 2: Life histories

2.1 Life history theory
The life history theory explains the interactions of natural selection, fitness, adaptation, and constraints and explains the broad features of life cycles. Life history analyses natural selection by considering variation in fitness, and looking at what causes these differences in fitness. In the life history theory, fitness is defined by r: the intrinsic rate of increase of a population, which is the growth rate per individual per unit of time. The intrinsic rate of increase is the number of births minus the number of deaths in a population with a high value having a high fitness due to a lack of deaths, and a value below zero, having a low fitness and a decline of population size. The fitness, or growth rate of a population, can be affected by many factors in life. These factors influencing fitness are called the life history traits (Stearns, 1992).

There are some principle life history traits that make up the phenotype. The key life history traits are: size at birth, growth pattern, age and size at maturity, number and size of offspring, reproductive investment and length of life. These life history traits can all affect fitness in their own way. For example the age at maturation can affect fitness directly. When an individual reaches maturity early and fecundity declines slowly with age, the offspring that subsequently starts reproducing at young age contributes to the fitness of the parent as well, by passing on part of its' genetic make up to the next generation (Stearns, 1992).

As mentioned before, energy cannot be spent on all fitness maximizing aspects of life simultaneously (Zafon, 2003). Life history traits are therefore connected by constraining relationships, called trade-offs (Stearns, 1992).
Individuals cannot invest in early maturation, high fecundity and late ageing at the same time. Common constraints are the trade-off between the number, size, and sex of the offspring, current reproduction and future reproduction, and the trade-off between reproduction and survival (Stearns, 1992).
All these trade-offs, and fitness affecting aspects, make up the life history. How individuals budget time and energy into achieving the highest fitness is crucial.

The greatest reproductive output would be achieved by starting reproduction at an early age, have large clutches and reproduce many times.

2.2 Optimality theory

The optimality theory suggests that organisms might have evolved an optimal life history which would be early reproduction, or high pre-adult survival at the cost of survival and fertility later in life (Partridge & Barton, 1993). This decline in survival and fertility are the effects of a fast rate of ageing, and are thought to be a side effect of early reproduction. The benefits of early reproduction are thought to be demographic (Bell, 1980 but see Stearns, 1992) because when less time is spend as a juvenile, individuals will have a higher probability to reach the age of maturity. The early reproducing individuals will also have a higher fitness due to the fact that their offspring are born earlier and will start reproducing sooner (Cole, 1954; Lewontin 1965; Hamilton 1966; but see Stearns, 1992). Varying strategies and life histories are found in different species, depending on the chance on extrinsic hazards, available resources and genetic make-up (Cichón & Kozlowski, 2000; Zafon, 2003). But if the optimal life history is reproducing early at the cost of survival later in life, then why has this strategy not evolved in all species and why can so many different reproductive strategies be found in nature?

Selection for a certain trait usually happens when this trait is evolutionary favorable to have under current circumstances, and is therefore adaptive. However for a preferred trait to become visible in a population, it is always dependent on genetic variation and the strength of evolutionary forces acting on it. The evolutionary equilibrium of any trait is thought to be the sum of the costs that reduce fitness, and the benefits that increase fitness. The costs of earlier maturation are the benefits of later maturation (Stearns, 1992) (Figure 2).

Benefits of earlier maturity:
Shorter generations
Higher survival to maturity because of shorter period as juvenile

Benefits of later maturity
Higher initial fecundity through longer growth
Lower instantaneous juvenile death rates
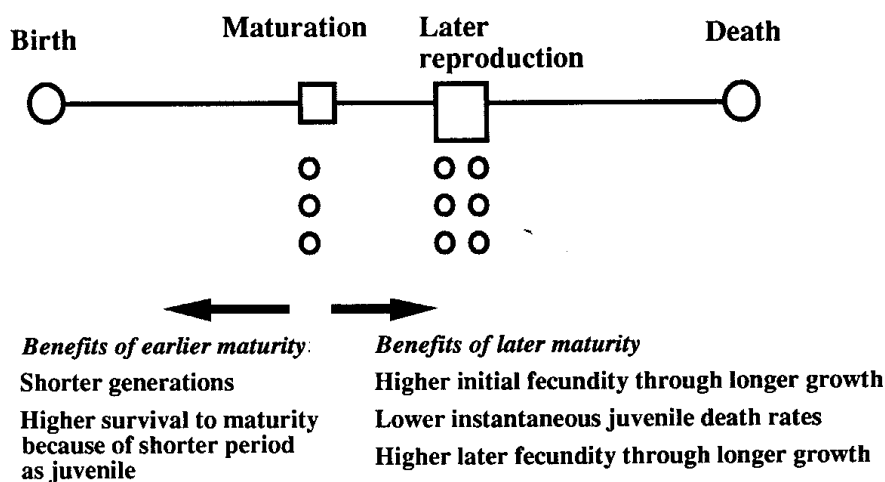Higher later fecundity through longer growth

Figure 2: A summary of the fitness affecting costs and benefits for either late or early maturation (Stearns, 1992).

Because the strengths of these costs and benefits differ for different species and even within species (Austad, 1993), the rate of ageing and the moment of

reproduction are often dependent on life history. It is common to find weaker organisms to reproduce early and strong organisms to reproduce late (Stearns, 1992).

To be able to illustrate why there might be differences in optimal reproductive strategies with differing ageing rates as an effect, two examples of different reproductive strategies are shown.

2.3 Early and late reproduction

For organisms that tend to be more susceptible for extrinsic hazards and face more extrinsic mortality, the chance of surviving to the age of maturity is relatively small. This would lead to natural selection for early maturation. This phenomenon is clearly demonstrated by the effects of unnatural selection by fishing on for example Northern Cod (Olsen et. al., 2004).

Cod that are maturing earlier in life are unnaturally selected for, by the effects of the fishing industries. This is because it is likely that only early reproducing individuals will produce offspring before they get caught, so only they will be able to pass on their genetic makeup. In this case there is selection for early reproduction. This example illustrates that often the trade-off between reproduction and ageing is shaped by selection for a certain phenotype that might be profitable for a population in a given environment. The optimal life history is determined by environmental factors and therefore the optimal ageing strategy shapes as an effect of natural selection on the optimal reproduction strategy.

Organisms that experience low extrinsic mortality, are more often found to reach maturation late in life (Stearns, 1992). Late reproduction has evolved because there are also advantages of late reproduction.

First of all, the delay of reaching maturity permits investment in for example body-size. Fecundity is known to increase with size and therefore delayed maturity will lead to a higher initial fecundity. This is one effect that might be more advantageous than the effects of early reproduction (Stearns, 1992).

Another effect might be that delayed maturity is probable to cause an increase in the quality of the produced offspring, or in parental care (Stearns, 1992). This means that there would be less juvenile mortality and this effect might outweigh the effects of earlier maturation until the point where the investment does not weigh up to the results.

These two life history strategies indicate that the optimality of a reproductive strategy is determined by many variable factors, such as the type of organism, the extrinsic hazards and the susceptibility thereof. It is not necessarily optimal to reproduce early in life, but the evolution towards a certain reproductive strategy is determined by many costs and benefits affecting fitness.

Life history shows that lifespan and reproduction are linked. The rate of ageing evolves as an effect of selection for an optimal reproductive strategy as proposed by the antagonistic pleiotropy theory (Williams, 1957). However it is the disposable

soma theory that predicts the direct link ageing and reproduction most direct by suggesting a trade-off in the allocation of limited resources (Kirkwood, 1977 but see Zafon, 2003).

Chapter 3: Resource allocation

The disposable soma theory points out the direct cause of the trade-off between ageing and reproduction: the allocation of limited resources. According to the optimality theory of Partride & Barton (1993, but see Novoseltev et. al., 2002) the individual that has the optimal balance between investment in reproduction and somatic maintenance will have the highest reproductive success (Figure 3) (Novoseltev et. al., 2002). To see till what extent resource allocation is the determining factor in the trade-off between ageing and reproduction, this chapter will emphasize on the research that has been performed to test whether there is resource allocation as proposed by the disposable soma theory, and if, if this is the case, this allocation is optimal.
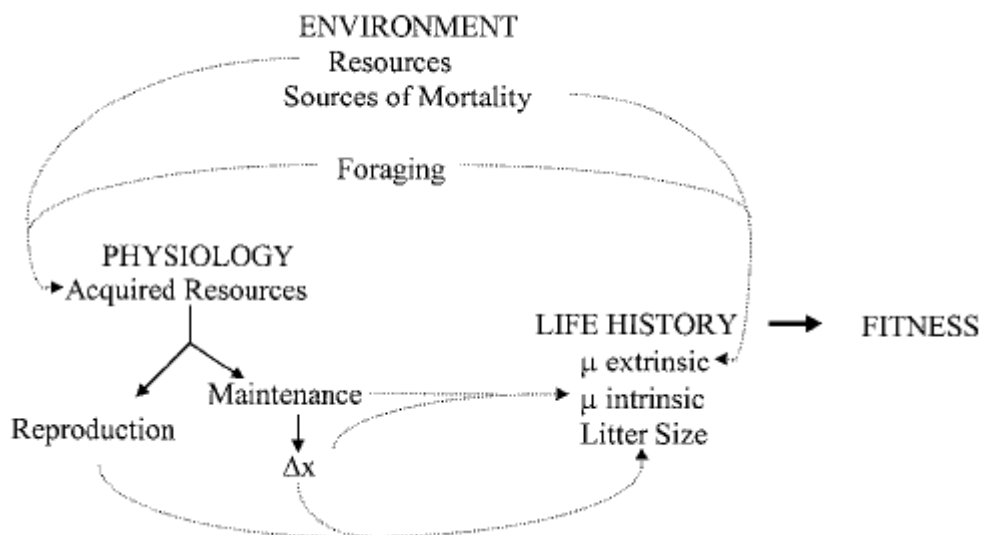

Figure 3: The effects of a dynamic optimization of resource allocation between maintenance and reproduction and life history, on fitness (Shanley & Kirkwood, 2000).

3.1 Costs of mating
According to the disposable soma theory there is a cost of investing in reproduction. One example that clearly illustrates the costs of mating was shown in a research by Chapman et. al. (1995). They showed that elevated rates of mating caused the

females to die younger than the controls. This was demonstrated to be caused by the effects of seminal fluid products from the main cells of the male accessory glands. Increasing exposure to these main cell products lead to an increase in female death rate.

This research shows that there are costs to mating and therefore reproduction. However a negative correlation between ageing and reproduction is not exclusively predicted by the disposable soma theory, but by the antagonistic pleiotropy theory as well (Williams, 1957). It is therefore necessary to find proof for the allocation of limited resources to either repair mechanisms or reproduction, in order to be able to propose part of the nature of the trade-off between ageing and reproduction.

3.2 A transitory phase

Research by Arking et. al. (2002) points out that there is a reduction in fertility as an effect of investment of resources in repair mechanisms, like proposed by the disposable soma theory (Kirkwood, 1977 but see Zafon, 2003; Drenos & Kirkwood, 2005). However, when selecting for longevity, the reduction in fertility showed to be merely a transitory phase in the run to achieving longevity.

In a selection experiment on *Drosophila melanogaster* (Arking et. al, 2002) where longevity and fecundity were compared, the first results applied to the evolutionary idea, in that there is a trade-off between fecundity and longevity. However, when looking at the data more closely, it became clear that the decline in fecundity with an increase of longevity had a stronger effect on the early eggs than on the later eggs. The decline in fecundity seemed to be a transient state only and later generations recovered to normal fecundity with larger longevity. Mathematical models showed that the control female's metabolic energy expenditure was on somatic maintenance and reproduction. The short-lived female suggests a lack of expenditure on somatic maintenance, which is consistent with the disposable soma theory. In the longevity female an increase in the amount of energy being used for somatic maintenance is found.

According to the theory, the longevity female with increased investment in somatic maintenance should have a reduced longevity. This however is only found in the first generations. The reduction in fertility in the first generations is thought to be caused by the need for metabolic reorganization so that this extra energy could be invested in improving the repair mechanisms. It is thought that the energy was spent largely on altering the maintenance system in such a way that both longevity and normal fecundity are possible.

The outcome of this research at first seems rather contradictory with the disposable soma theory in that there is not one long-term effect of an unbalanced resource allocation. Nevertheless, during the process of selecting for longevity, there is a trade-off between investing energy in either reproduction or somatic repair. This selection experiment is therefore largely consistent with the disposable soma theory in that the allocation of limited resources influences the rate of ageing and reproduction.

The research by Arking et. al. (2002) also answers the risen question: why do fruitflies not evolve to be both long-lived and fecund and reach an optimal life history? Long-lived *Drosophila* show a significant reduction in the exhibition of developmental viability, relative to the normal strains. They may lay the same number of eggs but there is a significant reduction in viable adults that came from the "long-lived-eggs". The increased longevity of the selected females seems to constrain the reproduction after all, since longevity females turn out to give rise to less viable adults than control females, resulting in a decreased fitness. The relatively higher fitness in the control females suggests that the natural balance in resource allocation might be optimal (Partridge & Barton, 1993 but see Novoseltev et. al., 2002).

3.3 Optimal resource acquisition and allocation

Another research that proves the role of resource allocation in achieving an optimal life history was performed by Novoseltev et. al. (2002), who looked at: energy uptake, reproduction and longevity. Resource allocation in *Drosophila* females in terms of oxygen consumption spend on reproduction and maintenance, was investigated. Results indicated that the experimentally found resource trade-offs were consistent with theoretical optimal trade-offs in allocation between maintenance and reproduction, indicating that there is not only resource allocation but that resource allocation is also close to optimal (Kirkwood, 1977 but see Zafon, 2003). In order to have an optimal life history (Partridge & Barton, 1993), there needs to be early reproduction, which requires high investment of resources in reproduction, and a high resource acquisition Novoseltev et. al. (2002).

However increased intake of resources is thought to be associated with an increased risk of somatic damage (Yearsly et. al., 2005). Due to a need for high resource acquisition on the one hand to reach an optimal life history, and an increased risk of somatic damage on the other hand, there needs to be an optimal resource acquisition as well as an optimal resource allocation.

Models on resource acquisition and allocation (Yearsly et. al.) indicate that an increase in mortality can be due to increased resource acquisition and not necessarily a decrease in the allocation to maintenance and repair as is predicted by the disposable soma theory. This assumption gives rise to the idea that the trade-off between ageing and reproduction might not be as direct as is predicted by the disposable soma theory, and the constraining factors of acquisition and allocation of resources might be intertwined in achieving an optimal life history. Nevertheless, the role of limited resources and the optimal allocation and acquisition thereof, is in the line with the life history theory in the idea that balancing constraints is the key factor in the race for the highest fitness.

Conclusion

According to the life history theory there is an ongoing dynamic trade-off in the allocation of resources. In this case, resources are like a pie that needs to be divided, and every fitness defining aspect will get a piece, either large or small.
Because mortality is often caused by extrinsic factors rather than intrinsic ones, there are several reproductive strategies found in nature, depending on fitness determining costs and benefits. The reaching of an optimal reproductive strategy is often the result of many environmental factors and also a factor of an individual's susceptibility to extrinsic mortality.
In the context of life histories there is often a trade-off between ageing and reproduction as an effect of the accumulation of antagonistic pleiotropic mutations. An individual that experiences high extrinsic mortality will face selection favouring early reproducing organisms. When removing the extrinsic hazards, selection will not necessarily favour early reproducing organisms because late reproduction can lead to a higher fitness (Stearns, 1992). The rate of ageing consequently evolves as an effect of selection for the optimal reproduction strategy. Ageing in this case is merely a result of reaching a high fitness. There is however a trade-off between ageing and reproduction due to a limited amount of energy that can be spend on fitness maximizing traits in life.

The disposable soma theory is the theory that best describes the direct link between ageing and reproduction, through the constraint in the allocation of resources. There are many researches that proof a trade-off between lifespan and reproduction (Smith 1959, but see Stearns, 1992; Novoseltev et. al., 2009; Arking et. al., 2002) and some researches suggesting that this is due to a constrained resource allocation (Arking et. al., 2002; Novoseltev et. al., 2002).
In order to be able to reach the optimal life history with early reproduction, early investment in reproduction is necessary and therefore a high resource acquisition is necessary (Novoseltev et. al.). But because resource acquisition also risks an increase of mortality due to oxidative damage (Yearsly et. al. 2002), there is another trade-off between acquiring high energy to invest in reproduction, and the consequence of possible larger somatic damage as a result. This assumption suggests that an increase in the rate of ageing due to investment in reproduction is not as direct as proposed by the disposable soma theory (Kirkwood, 1977 but see Zafon, 2003), but more a side-effect of high energy acquisition. The assumptions of costs of both energy acquisition and allocation are not mutually exclusive however, and there is most likely a dynamic link between life history choices, resource availability and acquisition and the allocation of resources. This dynamic link between intrinsic and extrinsic factors, are at the base of the trade-off between the process of ageing and reproduction in the context of life histories. Ageing and reproduction are not constant characters, and there will always be selection acting in order to create an optimal phenotype, at least for the moment.

Acknowledgements

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