

## Life History



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### Introduction

All living organisms, ranging from archaea and bacteria to fungi, plants, and animals, can be described through their life cycle, which is how and when they grow, mature, reproduce, and die. The description of the life cycle is what we define as the life history of a species. The study of the diversity of life histories allows us to understand the causes and consequences of the variation in life cycles that range from a few hours for some bacteria to a few centuries for some plant species. When it comes to understanding the tremendous diversity of life histories found in nature, two traits become particularly important: survival and fecundity. Indeed, the probability that an organism survives long enough to reproduce (juvenile survival), the probability that it survives long enough to do so repeatedly (adult survival), and the number of offspring produced at each reproductive event (fecundity) add up to determine the total number of offspring produced throughout the lifetime of an organism. Lifetime number of offspring provides an estimate of Darwinian fitness (the genetic contribution of an individual to the next generation's gene pool) and is

what natural selection ultimately acts on. Hence, variations in life history, and by extension variations in survival and fecundity, are molded by natural selection and expected to mirror adaptation of populations and species to their environment (Roff 1992; Stearns 1992).

Variations in life history and adaptation to the environment can be classified along a fast–slow continuum, with high reproductive rate and low survival at one end versus slow reproductive rate and high survival at the other end. Organisms with fast life histories thrive in unpredictable or unstable environments that cause large fluctuations in population growth rates ( $r$ ) and population sizes. Organisms with slow life histories, however, prosper in more stable environments thereby allowing their population sizes to be close to the maximum sustainable size in the given environment or carrying capacity ( $K$ ) (Oli 2004; Saether and Bakke 2000; Salguero-Gómez et al. 2016). In population ecology, fast and slow life histories are thus referred to as  $r$ - and  $K$ -strategies, respectively (MacArthur and Wilson 1967). Organisms with fast life histories include, among others, bacteria, annual plants (grasses), and small mammals (mouse), whereas organisms with slow life histories are well represented by perennial plants (trees) and large mammals (elephants and humans). Yet, most organisms' life history falls somewhere in-between a fast and a slow pace of life.

## Fitness and Life History Trade-Offs

Following the theory of evolution by natural selection, an organism should maximize its Darwinian fitness at any given time. Thus, an organism with highest Darwinian fitness would start reproducing directly after being born, reproduce continuously, produce an infinite number of offspring at each reproductive event, and live indefinitely. The existence of such an organism, the so-called *Darwinian demon*, presumes the absence of any constraints at all. However, all living organisms need energy and time to grow, maintain their bodies, and reproduce. In nature, resources are usually in limited supply, and there is often competition to access them (e.g., food patches for animals, access to sunlight and minerals for plants). When food is unlimited, such as during large migrations of prey species, in mast years of seed production, or under artificial conditions, there are still limitations on how much food an organism can ingest and in how efficiently it transforms energy enclosed in food into cellular energy, used to fuel its life cycle. Therefore, each organism is expected to have access to limited (non-infinite) resources that must be divided among life history traits such as growth, body maintenance, and reproduction. In addition, all biological, chemical, and physical processes take time to complete and have a specific order in which they need to be realized. Thus, each organism is also expected to be constrained in terms of when and how it should allocate its limited resources among different life history traits. How much energy and time is allocated to one life history trait at the expense of others is what defines a life history trade-off (Stearns 1992). As mentioned above, from an evolutionary perspective, the optimal solution to a life history trade-off is one that maximizes Darwinian fitness. There is, however, rarely a single solution to a given life history trade-off, and multiple solutions, depending on environmental conditions, are possible. As a consequence, solutions to a trade-off can greatly differ among species but also among populations within a species and among individuals within a population (McNamara and Houston 1996). Alternative solutions to a given life history

trade-off are defined as alternative life history strategies.

There are a large number of trade-offs that can be defined in the context of energy and time allocation to reproduction and survival. Some of the most important trade-offs that organisms face through their life cycle are (i) how fast and how long to grow before starting to reproduce, (ii) how often to reproduce and how much time and energy to invest in each reproductive attempt, and (iii) how to divide resources between offspring number and size.

### The Trade-Off Between Growth and Reproduction

The trade-off between growth and reproduction determines an organism's size and age at first reproduction. Some stages of the life cycle of organisms, specifically the early stages, are particularly vulnerable to predation. As the probability of dying from predation greatly declines when an organism increases in size, selection should favor individuals with a fast growth during the life stages most susceptible to predation. Furthermore, when predation remains important throughout the life cycle, selection is also expected to favor individuals that reach sexual maturity quickly and have an early onset of reproduction. Examples of the trade-off between growth and reproduction are found across fish species, where small species like guppies (*Poecilia reticulata*), which mainly feed on invertebrates, use their energy to grow fast and reproduce rapidly, but never attain the size that would give them defense against predators. Larger fish, like the Atlantic bluefin tuna (*Thunnus thynnus*) or the great white shark (*Carcharodon carcharias*), which are opportunistic predators, reach a large size but have a much delayed reproduction. In species that grow continuously throughout their life, selection will select for an optimal size at first reproduction following two conditions: first, fecundity needs to increase with size (e.g., female fish produce more eggs as they grow larger, and trees produce more seeds as they grow bigger); and second, growth rate needs to decrease after reproduction started, due to energy being allocated to both reproduction and growth rather than to growth alone. Age at

first reproduction in Atlantic cod (*Gadus morhua*) is a good example of the growth versus reproduction trade-off. A reduction in age at first reproduction of Atlantic cod has been observed with an increase in fishing pressure on larger-sized animals, which removed some of the benefits of growing large before reproducing for the first time (de Roos et al. 2006; Rowell 1993). Similarly, an optimal size at first reproduction is also expected in species that do not grow continuously but where individuals could start to reproduce before completing body growth. In bighorn sheep (*Ovis canadensis*), where females could start to reproduce at 2 years old and grow until 6 years old, age at first reproduction is strongly affected by body size suggesting an optimal size for first reproduction (e.g., Martin and Festa-Bianchet 2012).

### The Trade-Off Between Current Reproduction and Survival

The trade-off between current reproduction and survival posits that the amount of resources allocated to immediate reproduction at the cost of survival will be justified by the probability of reproductive success. It is therefore expected that the frequency and amount of reproduction are negatively correlated with the longevity of a species. It is easy to think of circumstances under which reproduction could lead to decreases in survival. Reproductive individuals might be more visible (e.g., birds' plumage colors during reproduction, mating displays and calls that attract both mates and predators), more active, slower, or less agile than nonreproductive individuals and thus may suffer higher risk of predation. Higher risk of predation due to reproductive behavior can arise in four different ways. First, predators or parasites may detect mating calls or mating displays such as opossums locating mate calling frogs (Ryan et al. 1981). Second, instead of detecting mating calls, predators might attract prey by mimicking their mating calls. In fireflies, females of the species *Photuris versicolor* attract and predate male of other firefly species by mimicking the mating flashes of other female species (Lloyd 1975; Lloyd and Wing 1983). Third, the increase in activity linked to reproduction might

increase an animal's predation risk by either making it more visible or by simply increasing its probability to encounter predators. In tick-tock cicadas (*Cicadetta quadricincta*), mate-seeking males are more frequently captured by web-building spiders than females are (Gwynne 1987). Fourth, defense of young by parents might place a reproductive individuals at higher risk of predation when the predator can prey upon both parents and the offspring. In sticklebacks, males guard and defend the brood against fish predation (Pressley 1981). In addition to an increase in predation-related mortality, reproductive individuals might be exposed to a higher risk of death by disease, if the energy invested in reproduction is diverted from the immune system and physiological maintenance of the organism. Thus, trade-offs between current reproduction and survival are linked to trade-offs between reproduction and body condition, since most of the time a decrease in survival probability after reproduction is due to a decrease in overall body condition. Furthermore, the trade-off between reproduction and survival is strongly linked to the trade-off between current and future reproduction since an individual must survive in order to reproduce in the future.

### The Trade-Off Between Offspring Quantity and Quality

Once an individual commits to reproducing, given the set amount of energy it can allocate to reproduction, a major trade-off is the trade-off between offspring quantity and quality. This concept considers that offspring survival is dependent on their "quality," e.g., body size. Thus, in order to maximize Darwinian fitness, the limited amount of resources invested in reproduction should be maximized as a function of number of offspring and offspring quality. Should the majority of energy be invested in producing only one sizeable offspring or multiple smaller offspring? When offspring survival is low, two main strategies could arise to maximize the probability of offspring reaching maturity. First, if increasing the size of an offspring increases its survival, then producing fewer, larger offspring would be adequate. However, this is also a risky strategy since only a few

offspring are produced. The second strategy to counterbalance low juvenile survival is not to try to increase juvenile survival but simply to produce an extremely large number of offspring, thus leading to a high probability of having some offspring reaching maturity. Orchids are a good example for the strategy of producing large numbers of offspring with minimum energy invested per individual offspring, given that orchids have the smallest seeds of all flowering plants and produce millions of them. An orchid seed has virtually no reserves and relies on symbiotic interactions with a fungus to develop (Kull et al. 2009). On the other hand, flowering plants such as the coco de mer (*Lodoicea maldivica*) produce only a few seeds, but each seed weighs between 15 and 30 kg, allowing them to germinate and grow on really poor-quality soil. The trade-off between number and size of offspring could also be observed within species. A classic model for this trade-off is Lack's clutch size in birds (Lack 1954), which illustrates that there are an optimal number of offspring to produce. The model stipulates that if the survival probability of an offspring decreases as the number of offspring produced increases, then there are an optimal number of offspring that maximize the number of offspring surviving. The decrease in offspring survival probability with larger clutch size could be due to a decrease in egg size or an increase competition between offspring for parental care.

### Life History Trade-Offs and the Evolution of Viviparity and Parental Care

Increasing the size of the egg or the offspring is not the only strategy to maximize the number of surviving offspring. The probability of an offspring surviving until adulthood is an important parameter linked to a number of different trade-offs. Since juvenile survival has a direct impact on Darwinian fitness, strategies to increase early survival are under strong selection. The evolution of different modes of reproduction, from oviparity to ovoviviparity and viviparity, was driven also by life history strategies that allow reducing early juvenile mortality and favoring the production of

fewer offspring but of higher quality. Oviparous animal species lay eggs that contain high amount of nutriment and that develop outside the body cavity of their mother. In ovoviviparous species, the embryo is still relying on resources enclosed in the egg for its development, but the eggs are retained inside the female's body cavity until they are ready to hatch. It allows reducing exposure to predation and pathogens during the egg stage. Finally, viviparous species produce very small eggs that have few or no nutrients, the embryo must feed on resources passed on from the mother during development, and thus mothers give birth to live offspring. It allows the production of larger and more mature offspring, further reducing the costs of predation and pathogen exposures. Generally, the same is true for the evolution of any form of parental care that reduces juvenile mortality and permits greater investment in fewer, larger offspring (Clutton-Brock 1991; Royle et al. 2012).

### Life History Trade-Offs in Semelparous and Iteroparous Reproductive Strategies

Life history traits, such as fecundity, timing of reproduction, size and number of offspring, and parental care, can be grouped together into general reproductive strategies that are used by multiple species. Semelparity occurs when a species reproduces only once during its lifetime, produces a large number of offspring, and then dies. Semelparity is thus also known as "big bang" reproduction. Semelparous species accumulate resources and use them during a single reproductive event, detrimental to their own condition, to the point that they do not survive. Semelparity is seen in annual plants, in long-lived plants such as agaves, in many species of fish such as salmon, in insects, and in mollusks, but rarely in large vertebrates. Iteroparity describes species that reproduce repeatedly during their lifetime. Some animals are able to mate only once per year but survive through multiple mating seasons. Most perennial plants are iteroparous, as are most mollusks, insects, and vertebrates, including most reptiles as well as virtually all mammals, birds,

and most fish. Semelparous and iteroparous strategies are the result of alternative prioritization of life history trade-offs. In semelparous organisms the main trade-off is how much an organism should grow before reproducing, given that size and fecundity are related, whereas in iteroparous organisms, the main trade-off is how much to invest in each reproductive event versus maintenance and survival.

### Acquisition and Allocation of Resources in Life History Trade-Offs

While studies of life history trade-offs have been highly successful at illustrating trade-offs comparing multiple species and using a phylogenetic approach, studies of trade-offs within species are often more problematic. Life history trade-offs are, by definition, a compromise in resource allocation. However, not all individuals acquire the same amount of resources, a notion known as individual heterogeneity in resource acquisition. When among-individual variation in resource acquisition is small relative to the variation in resource allocation to reproduction and survival, then a trade-off between survival and reproduction could be observed (van Noordwijk and de Jong 1986). On the other hand, when variation in energy acquisition is large relative to the variation in energy allocation, a positive correlation between survival and reproduction is observed instead of a trade-off. As an example, when testing for trade-offs between growth and reproduction, there may be no apparent trade-offs if size and resource acquisition covary, and thus larger individuals have more resources than smaller individuals to invest in both growth and reproduction (Reznick et al. 2000). However, once the variation in size or resource acquisition is controlled for, either experimentally or statistically, trade-offs should become apparent (Reznick et al. 2000). Thus, when studying life history trade-offs, it is important to understand and consider the existence of individual heterogeneity (Tettamanti et al. 2015).

The amount of available resources for organisms to acquire and allocate to life history traits

frequently varies with environmental conditions in either a predictable or an unpredictable manner. In a variable and predictable environment, being able to adjust resource allocation according to environmental conditions and thus to resource acquisition is key to maximizing Darwinian fitness. The capacity to respond differently to different environmental conditions is referred to as phenotypic plasticity. Phenotypic plasticity in life history traits is observed in a wide range of species. For example, spring temperature is a good predictor of timing of food availability in insectivorous great tits (*Parus major*), and the date on which adults lay their eggs varies as a function of spring temperature. This allows synchronization of the hatching date of individuals' clutches with the date of peak caterpillar abundance, thus optimizing resource availability for offspring growth and fitness (Charmanier et al. 2008).

### Mechanisms of Life History Evolution

For life history traits to evolve, they must have a genetic basis. Hence, our understanding of the evolution of life history trajectories also requires an understanding of the genetic, molecular, and physiological pathways that link the genotype to the phenotype. A main assumption of life history theory is that trade-offs are generated by competitive allocation of resources, with the allocation of limiting resources to one trait having negative consequences for other traits requiring the same resources (Flatt and Heyland 2011; Zera and Harshman 2001). As a consequence, the diversification of life histories is closely linked to all the molecular and physiological activities that regulate the flow of energy through the body of organisms – that is to say their metabolism. Variation in the secretion of hormones with strong effects on the metabolism and on life history trade-offs is thus one of the mechanisms underlying the integration of life history traits. In animals, this includes steroid hormones such as the male hormone testosterone and the stress hormone corticosterone, which both regulate the trade-off between reproduction and survival, and metabolic

peptides such as the insulin-like growth hormone that regulates the trade-off between growth and somatic maintenance (Flatt and Heyland 2011; Zera and Harshman 2001). Remarkably, genes encoding for such hormones and their receptors, which match growth and reproduction to nutrient supply, have been found to be evolutionarily conserved in the animal kingdom, ranging from organisms such as the budding yeast (*Saccharomyces cerevisiae*), the nematode worm (*Caenorhabditis elegans*), and the fruit fly (*Drosophila melanogaster*) to humans (Flatt and Heyland 2011). Mechanistic explanations of life history trade-offs do not rely uniquely on competitive resource allocation, and systems such as metabolic waste management can also generate non-resource-based trade-offs. For example, in aerobic organisms, the transduction of energy from food to cellular energy during mitochondrial respiration has, as an inevitable side effect, the production of reactive oxygen species that can damage the soma as well as reduce organism reproduction and survival (Monaghan et al. 2009). Indeed, when the production of reactive oxygen species outweighs the cellular antioxidant defenses, organisms are exposed to oxidative stress. This stress can mediate life history trade-offs, such as that between reproduction and survival, if the processing of resources allocated to reproduction creates an oxidative debt on survival (Monaghan et al. 2009; Stier et al. 2014).

## Life History and Behaviors

For a long time, animal behaviors have been poorly considered when studying life history and natural selection. However, the emergence of research on animal personalities has led to both the development of new theories and the accumulation of evidence about the importance of behaviors in shaping species' life histories (Réale et al. 2009; Martin et al. 2014). In particular, the existence of feedback loops between behaviors and life histories or morphological traits has been shown to provide an adaptive explanation for the evolution of animal personality and for the development of life histories (Wolf et al. 2007). For

example, individuals with high expectations of future reproduction, that have much to lose, should be more risk-averse than individuals with low expectations. In addition, being more risk-averse increases survival probability and thus by definition increases expectations of future reproduction. This creates a positive feedback loop where the behavior and life history strategy are reinforcing each other.

Studies on sexual selection also illustrate important correlation between life history and behaviors with the existence of alternative mating strategies (Réale et al. 2009). Alternative mating strategies are usually defined by alternative mating behaviors, allowing the emergence of alternative reproductive and life history strategies. A good example is the difference between different mating strategies in the Atlantic salmon (*Salmo salar*). Dominant males grow rapidly, migrate to sea, delay maturation, and mate guard females whose eggs they can easily fertilize. Sneaker males do not migrate to sea, have limited growth, have early maturation, cannot mate guard females, and have to avoid mate-guarding males to try and fertilize females' eggs. However, they can outcompete dominant males in sperm competition for fertilization by producing higher-quality sperm (Vladić and Petersson 2015).

## Conclusion

Life history theories state that organisms maximize their Darwinian fitness through optimization of their life history traits as a function of multiple trade-offs. The study of life history trade-offs and of the diversity of life histories helps to understand the main selection pressures that organisms are facing in addition to why and how they are adapted to their environment. To gain insights on the diversity of life histories, it is important to not only understand the ultimate consequences of trade-offs but to also understand the proximate mechanisms underlying them. Finally, life history traits are not limited to morphological and reproductive traits but include physiological and behavioral traits. The pace-of-life syndrome hypothesis specifies that a suite of metabolic,



hormonal, immunity, and behavioral traits have coevolved with life history particularities related to different ecological conditions (Réale et al. 2010). This hypothesis therefore provides an integrative framework to study both proximate mechanisms of behaviors and their ultimate consequences for life history evolution.

## Cross-References

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- [Additive Genetic Variance](#)
- [Arthropod Life History](#)
- [Artiodactyla Life History](#)
- [Bear Life History](#)
- [Bovine Life History](#)
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- [Swine Life History](#)
- [Testudines Life History](#)

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