



Review

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Early-late life trade-offs and the evolution of ageing in the wild

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Empirical evidence for declines in fitness components (survival and reproductive performance) with age has recently accumulated in wild populations, highlighting that the process of senescence is nearly ubiquitous in the living world. Senescence patterns are highly variable among species and current evolutionary theories of ageing propose that such variation can be accounted for by differences in allocation to growth and reproduction during early life. Here, we compiled 26 studies of free-ranging vertebrate populations that explicitly tested for a trade-off between performance in early and late life. Our review brings overall support for the presence of early-late life trade-offs, suggesting that the limitation of available resources leads individuals to trade somatic maintenance later in life for high allocation to reproduction early in life. We discuss our results in the light of two closely related theories of ageing—the disposable soma and the antagonistic pleiotropy theories—and propose that the principle of energy allocation roots the ageing process in the evolution of life-history strategies. Finally, we outline research topics that should be investigated in future studies, including the importance of natal environmental conditions in the study of trade-offs between early- and late-life performance and the evolution of sex-differences in ageing patterns.

1. Introduction

Patterns of senescence¹ (i.e. the decline in fitness components with age) are highly variable both within and among species (e.g. [1–3]). Understanding the selective forces shaping this variation has become a key topic in the study of ageing [4,5]. Medawar [6] initially proposed that senescence comes from the accumulation of deleterious mutations that are expressed late in life, when the forces of natural selection are weaker and prevent these mutations from being purged [6]. Hamilton formalized Medawar's ideas by demonstrating that senescence could arise because of the decreasing strength of natural selection with age, starting from age at sexual maturity ([7] but see [8]). Hamilton concluded that senescence is inevitable for all age-structured populations [7], including most vertebrate populations [9]. Medawar's pioneer work has also been expanded by Williams who proposed the antagonistic pleiotropy theory of ageing, which states that an allele with a negative effect on performance in late life could be selected if it has a positive effect on reproduction during early life [10]. Relationships between reproduction and body growth early in life and late-life performance are also at the core of the disposable soma theory of ageing introduced by Kirkwood [11]. This latter hypothesis proposes that individuals should optimize their resource allocation between body growth, reproductive expenditures and the set of mechanisms involved in the maintenance of their soma (e.g. enzyme-based repair mechanisms) as a function of their average lifespan or their risk of environmentally driven mortality [12]. When resources are allocated to reproduction rather than to somatic maintenance, molecular errors should accumulate more rapidly in somatic cells, leading reproduction or survival to decline faster as individuals age (i.e. a

stronger senescence) [12,13]. It is generally considered that both antagonistic pleiotropy and disposable soma theories of ageing lead to similar predictions in terms of life-history trade-offs between allocation to reproduction during early life and intensity of ageing in late life [12,14,15].

A large number of studies challenging predictions of a trade-off between allocation to body growth and reproduction in early life and fitness-related traits (survival and reproduction) in late life were conducted in the laboratory [16]. Until quite recently, senescence was thought to be almost absent in wild populations [5], which provides the most likely explanation for the long-standing focus on laboratory models. However, the situation is changing thanks to the accumulation of long-term individual monitoring of known-aged animals in the wild, which are providing increasing evidence of senescence in a wide range of traits in free-ranging conditions [5] and offer the necessary material for testing evolutionary theories of ageing in the wild. Empirical tests of early-late life trade-offs in the wild (compiled in table 1), where food availability and energy acquisition are generally limiting, are particularly relevant because individuals living under laboratory or captive conditions are usually fed *ad libitum*, which can potentially mask any trade-off between early- and late-life performance [5,43]. However, whether these study cases provide overall support for an early-late life trade-off remains to be assessed.

In this review, we first compiled studies that looked for early-late life trade-offs and we quantified the overall support for a negative covariation between allocation to body growth and reproduction during early life and fitness-related traits in late life. We then discussed whether such trade-offs match evolutionary theories of ageing. Finally, we propose new avenues of research for studies investigating early-late life trade-offs in the wild that should refine our understanding of both the influence of environmental conditions on ageing patterns and the evolution of sex-differences in ageing. Purposely, we limited the scope of our review to wild vertebrate species because most of these species are strongly age-structured, which fit evolutionary models of senescence and also because longitudinal studies on invertebrates in the wild remain scarce.

2. Tests of early-late life trade-offs in the wild

(a) Results of the literature survey

To find all published papers testing for a trade-off between allocation to body growth or reproduction early in life and allocation to survival or reproduction late in life in wild populations of vertebrates, we used a strict search protocol (see the electronic supplementary material). This protocol allowed us to identify 26 studies in 24 vertebrate species (12 birds, 10 mammals and two reptiles, table 1). Fishes and amphibians were absent from the compiled papers, which might be owing to the scarcity of long-term individual-based studies of these species in the wild [44] and to the difficulty of detecting senescence in species with indeterminate growth [45].

Our literature survey revealed that more than three-quarters (21 out of 26 studies, see table 1) of the studies provided support for the expected trade-off, which is statistically supported by a sign test ($p = 0.002$). Most authors concluded that evidence for a trade-off between allocation to

body growth or reproduction in early life and allocation to survival or reproduction in late life was supported when at least one of the negative correlations was statistically significant. When looking specifically at the number of relationships tested across the 26 studies ($n = 74$ relationships), a sign test revealed a statistically significant overall support for an early-late life trade-off ($p = 0.005$; 43 negative relationships, 20 positive relationships and 11 where the information was not available in the paper (i.e. only the statistical significance was reported)). For instance, in both free-living jackdaws (*Corvus monedula*) and red deer (*Cervus elaphus*), individuals with the highest reproductive effort during early adulthood senesced the fastest in terms of actuarial and reproductive performance, respectively [28,31]. It is worth noticing that a publication bias in favour of statistically significant results could potentially lead to an over-representation of the occurrence of trade-offs [46]. We also showed that the probability of finding a statistical support within a study for a statistically significant negative correlation between early and late life traits was not related to the number of tested relationships (electronic supplementary material, table S2). In addition, by fitting generalized linear mixed models including the focal study as a random effect, we observed that the statistical support for a trade-off between early and late life is less likely in mammals than in birds (electronic supplementary material, table S3).

(b) Early-life traits

Recovered studies have assessed a wide array of traits, which prevented us performing a formal and accurate meta-analysis (e.g. [47]). Age at first reproduction was the most commonly used metric to describe allocation to reproduction early in life (table 1). Many correlations between early reproduction and late-life performance were not negative on statistical grounds. Sometimes, early reproductive allocation was associated with higher performance later in life (table 1). For instance, red deer females giving birth at the earliest ages produce heavier offspring at late ages [31]. This suggests that early reproduction might reflect individual quality (*sensu* [48]), which prevents the expected trade-off to be revealed. Testing for long-term costs of reproduction requires accurate measures of energy allocation to the reproductive effort. Moreover, traits that are used to describe this type of allocation need to display some variability among individuals within a given population and age at first reproduction varies only little in some species. For instance, in roe deer (*Capreolus capreolus*), almost all females give birth at 2 years of age, even when the environmental conditions strongly deteriorate [49]. However, when scrutinizing the published correlations between age at first reproduction and late-life traits, a sign test reveals that early reproduction is often associated with long-term costs ($p = 0.008$, $n = 33$ relationships with 22 negative relationships, seven positive relationships and four relationships where the information was not available in the published study).

Studies investigating allocation to body growth remain rare from the compiled data (but see [29,42]). So far, most studies linking fast growth and performance in late life have been performed in laboratory conditions [50]. For example, in the three-spined stickleback (*Gasterosteus aculeatus*), fast-growing individuals have shorter longevity, which suggests that energy allocation to body development early in life leads to increased actuarial senescence [51]. Moreover, individuals that allocate strongly to reproduction early in life have often

Table 1. Summary of the 26 studies testing for early-late life trade-offs in vertebrate populations. (The species, the early and late traits analysed, the sex (F: female, M: male), the overall conclusion about the support for each study (yes/no) and the references are provided. For the column 'relationship', the '−' represents the negative relationship (in other words a trade-off between early and late traits), the '+' represents the positive relationship between early and late traits and the '0' represents the absence of a statistically significant relationship between early and late traits. However, when the sign of the non-significant relationship was provided in the study, this information was added in brackets, next to the '0'.)

| species | early trait | late trait | sex | relationship | early-late life trade-off detected | ref |
|------------------------|---|--|-----|--------------|------------------------------------|------|
| birds | | | | | | |
| western gull | age at first reproduction | survival | F | − | yes | [17] |
| | age at first reproduction | survival | M | − | | |
| | age at first reproduction | cumulative chicks fledged | M | − | | |
| | age at first reproduction | cumulative chicks fledged | F | − | | |
| willow tit | breeding status | late survival | M | 0 (−) | yes | [18] |
| | breeding status | late survival | F | − | | |
| chough | clutch size (3–4 years) | female breeding lifespan | F | − | yes | [19] |
| | fledging success (3–4 years) | female breeding lifespan | F | − | | |
| | breeding failure (3–4 years) | female breeding lifespan | F | 0 | | |
| | clutch size (5–8 years) | female breeding lifespan | F | 0 | | |
| | fledging success (5–8 years) | female breeding lifespan | F | 0 | | |
| tawny owl | age at first reproduction | adult survival | M | − | yes | [20] |
| | age at first reproduction | adult survival | F | − | | |
| blue-footed booby | recruit age | age at last reproduction | M | − | yes | [21] |
| | recruit age | age at last reproduction | F | 0 | | |
| | recruit age | breeding success | M | − | | |
| | recruit age | breeding success | F | 0 | | |
| | recruit age | brood size | M | − | | |
| | recruit age | brood size | F | 0 | | |
| common murre | early-life reproductive output | senescence in breeding success | F | − | yes | [22] |
| | early-life reproductive output | lifetime breeding success | F/M | − | | |
| mute swan | age at first reproduction | age at last reproduction | M/F | − | yes | [23] |
| collared flycatcher | age at first reproduction | clutch size | F | − | yes | [24] |
| great tit | early-life fledgling production | rate of late life age-specific change in number of fledgings | F | − | yes | [25] |
| | early-life fledgling production | rate of late life age-specific change in number of recruits | F | 0 (−) | | |
| | early-life reproduction | reproductive lifespan | F | 0 | | |
| black-legged kittiwake | age at first reproduction | breeding success | M/F | − | yes | [26] |
| Seychelles warbler | age at first breeding | onset of actuarial senescence | M/F | − | yes | [27] |
| | age at first breeding | rate of actuarial senescence | M/F | 0 (−) | | |
| jackdaw | brood size | annual survival rate | M/F | − | yes | [28] |
| | brood size | rate of actuarial senescence | M/F | − | | |
| mammals | | | | | | |
| bison | age at first reproduction | offspring number | F | + | yes | [29] |
| | weight at 0.5 years | fecundity during the first 7–9 years | F | − | | |
| red deer | age at first reproduction | actuarial senescence | F | + | yes | [30] |
| | early-life (less than 9 years old) reproduction | reproductive senescence | F | − | | |

(Continued.)

Table 1. (Continued.)

| species | early trait | late trait | sex | relationship | early-late life trade-off detected | ref |
|----------------------------|--|--------------------------------------|-----|--------------|------------------------------------|------|
| | age at first reproduction | calving date | F | + | yes | [31] |
| | age at first reproduction | offspring birth weight | F | + | | |
| | early-life fecundity | senescence in calving date | F | – | | |
| | early-life fecundity | senescence in offspring birth weight | F | – | | |
| | mean early calving date | senescence in calving date | F | + | | |
| | mean early offspring birth weight | senescence in offspring birth weight | F | + | | |
| | mean harem size | senescence in harem size | M | – | yes | [32] |
| | mean harem size | senescence in antler morphology | M | – | | |
| | allocation to antlers | senescence in harem size | M | 0 (–) | | |
| | allocation to antlers | senescence in antler morphology | M | 0 (–) | | |
| Weddell seal | age at first reproduction | survival | F | 0 (–) | no | [33] |
| rhesus macaque | age at first reproduction | survival to 11 years of age | F | – | yes | [34] |
| | age at first reproduction | survival to 16 years of age | F | – | | |
| | age at first reproduction | survival to 21 years of age | F | 0 (–) | | |
| | age at first reproduction | survival to 26 years of age | F | 0 (–) | | |
| badger | age at first reproduction | age at last reproduction | M/F | – | yes | [35] |
| bighorn sheep ^a | number of lambs produced | longevity | F | + | no | [36] |
| | number of lambs weaned | longevity | F | + | | |
| | number of lambs surviving to 1 year of age | longevity | F | 0 (+) | | |
| | number of lambs produced | number of lambs weaned | F | + | | |
| | number of lambs weaned | number of lambs weaned | F | + | | |
| reindeer | age at first reproduction | survival | F | + | no | [37] |
| greater horseshoe bat | breeding status | mean age at death | F | – | yes | [38] |
| | breeding status | breeding frequency | F | + | | |
| Columbian ground squirrel | age at first successful rearing | longevity | F | 0 (–) | no | [39] |
| | age at first successful rearing | lifetime reproductive success | F | 0 (+) | | |
| red squirrel | age at first reproduction | longevity | F | – | yes | [40] |
| | age at first reproduction | juvenile weaned per breeding attempt | F | + | | |
| reptiles | | | | | | |
| common lizard | reproductive effort | actuarial senescence | F | – | yes | [41] |
| | reproductive effort | senescence in litter size | F | 0 | | |
| | reproductive effort | senescence in offspring body size | F | 0 | | |
| | reproductive effort | senescence in litter success | F | + | | |
| garter snake | body growth tactic (slow vs fast) | senescence in litter mass | F | + | no | [42] |
| | body growth tactic (slow vs fast) | senescence in litter size | F | + | | |
| | body growth tactic (slow vs fast) | senescence in offspring mass | F | 0 (–) | | |
| | body growth tactic (slow vs fast) | senescence in relative clutch size | F | + | | |
| | body growth tactic (slow vs fast) | stillborn number | F | 0 (+) | | |

^aIn this study, two populations are considered (Ram Mountain and Sheep River) but the relationships between both the number of lambs produced and the longevity and the number of lambs weaned and the longevity are statistically significant at Ram Mountain only.

grown fast over this period [50], which might increase cellular damage even more and thereby accelerate senescence. In many vertebrates, early reproduction is often associated with a high growth rate because body mass generally determines social rank and success in sexual competition in males and the ability to ovulate in females [50]. Longitudinal studies in the wild should thus now seek to decipher the relative influence of

body growth and reproduction in shaping performance in late life.

(c) Late-life traits

For late life, we can distinguish three categories of measures of performance, corresponding to survival (e.g. longevity, rate of actuarial senescence), reproduction (e.g. rate of senescence in

reproductive success measured at different stages), or both reproduction and survival (e.g. age at last reproduction, lifetime reproductive success, table 1). Several correlations between early- and late-life traits have been tested within the same study, revealing contrasting results with respect to potential trade-offs. For example, in the female common lizard (*Lacerta vivipara*), a high reproductive effort during early life does not influence senescence in litter size but increases senescence in survival [41], in line with evidence that senescence patterns in life-history traits are heterochronous [4,52]. These results suggest that a high reproductive effort early in life can negatively influence only one aspect of the late-life performance (e.g. longevity or reproductive output). When we tested whether support for the early-late trade-off was more likely to be detected by using survival, reproductive performance or a metric combining survival and reproduction as the late-life trait, no statistically significant differences were found (electronic supplementary material, table S4), even after accounting for a putative taxonomic effect (electronic supplementary material, table S5). Recently, Hamel *et al.* [53] proposed a generalization of the Van Noordwijk & de Jong [54] Y-model (see also §3c), accounting for differential constraints in the variability of survival and reproduction observed in the wild. This model suggests that costs of reproduction are more likely to impact future reproductive performance in long-lived species because adult survival is environmentally canalized in these species [55], whereas costs of reproduction are more likely to impact future survival in short-lived species. Such questions are particularly relevant as the relative strength of reproductive and actuarial senescence can alter the general fitness costs of senescence [56]. When testing these predictions on a set of studies investigating short-term costs of reproduction (i.e. influence of reproduction at time t on survival or reproduction at time $t + 1$), Hamel *et al.* [53] found support for their model predictions. Interestingly, the predictions seem also to hold for cumulative costs of reproduction, although the number of studies was limited [53], particularly in short-lived species (as highlighted by the absence of any small-sized rodent in table 1). Detailed longitudinal data on short-lived species are now badly needed to test whether substantial allocation to body growth or reproduction during early life is more likely to increase reproductive senescence in long-lived than short-lived species.

(d) Tests of early-late life trade-offs in females and males

Most (83.3%) of the relationships explored in a single sex were performed on females (55 out of 66 relationships where the analysis are performed on one sex only), probably because it is easier to measure reproductive effort for this sex (e.g. [37]). Measuring male reproductive senescence (e.g. senescence in sperm quality, secondary sexual traits or reproductive success), longitudinally is currently extremely difficult in wild populations of vertebrates. However, such studies could potentially bring further support for a decrease in residual late-life fitness following high early allocation to reproduction, as suggested by recent work in captive houbara bustards (*Chlamydotis undulata*) where males with a higher display rate during early life senesce faster in terms of sperm number and motility [57]. Moreover, analysing the relationships compiled in table 1 using a generalized mixed effect model reveals that the trade-off is found more often in males than in females

(electronic supplementary material, table S6). This comes from the fact that among the few studies focusing on males, nearly all of them provided a support for a trade-off. However, contrasting patterns can sometimes emerge when senescence is investigated jointly in males and females. For instance, in willow tits (*Parus montanus*), early reproduction and survival in late life are independent in males, whereas females that do not breed during early life survive better in late life [18]. Overall, this emphasizes the need to test evolutionary theories of ageing in both sexes to identify the nature of the reproductive costs that influence performance in late life, and then the evolution of sex-differences in ageing patterns (see §4b for a specific discussion on this topic).

(e) How should we interpret studies in which the trade-off is not detected?

Five studies we reviewed (including four on mammals) did not report any statistical support for early-late life trade-offs (table 1). There are several possible explanations for this absence of support. First, high reproductive expenditures early in life may not be associated with long-term costs such that senescence patterns or longevity are independent of the amount of reproductive allocation in these species. Second, in these populations, individuals might live in high-quality environments, where abundant resources might make any life-history trade-off more difficult to detect [5]. Finally, inappropriate methodological tools could be involved. The existence of poor-quality individuals that died early in life can simply explain such failure to detect long-term costs of high allocation to reproduction. Interestingly, none of these studies controlled for individual heterogeneity although such variability in quality among individuals is likely to mask within-individual reproductive costs (e.g. when individuals with better than average reproductive success live longer than individuals with lower than average reproductive success [58]). In addition, selective (fertility selection or viability selection) or random (stochastic events) processes can favour the over-representation of individuals with high reproductive performance in late life. This can eventually hide any long-term costs of heavy allocation to reproduction in early life on survival and reproduction late in life [59]. However, when splitting studies between those that corrected for individual heterogeneity ($n = 8$ studies with eight finding a support for an early late-life trade-off) and those that did not correct for individual heterogeneity ($n = 18$ studies with 13 finding a support for an early late-life trade-off), a Fisher exact test revealed no association between the probability to find a support and the use of a statistical correction for individual heterogeneity ($p = 0.28$). Indeed, while studies accounting for individual heterogeneity led to a full support for the trade-off (100%), the relative amount of support remains high in the subset of studies that did not take into account this issue (72.2% instead of 80.8% for the whole dataset).

Overall, our literature survey reveals very good support for the occurrence of early-late life trade-offs in wild vertebrate populations. These phenotypic correlations between life-history traits could at first glance provide support for several evolutionary theories of ageing. In the following section, we discuss whether results from studies compiled in this review match or do not match these theoretical frameworks.

3. Early-late life trade-offs and evolutionary theories of ageing

(a) Disposable soma theory

One fundamental tenet of the disposable soma theory is the limitation in the amount of energy an individual can extract and process from its environment [12]. This leads individuals to share their finite pool of resources among body growth, reproduction and maintenance [13]. In Kirkwood and Rose's own words: *an organism is an entity that takes in resources from its environment, [...], uses these resources for a variety of metabolic tasks such as growth and maintenance, and in due course reproduces to generate an output of progeny. The problem of allocation of resources arises because resources used for one purpose are no longer available for other purposes* (see [12, pp. 16]). Therefore, individuals that allocate a substantial quantity of resources for reproduction will have to reduce their allocation to somatic maintenance [12], which will ultimately promote a faster senescence [12,13]. The same reasoning applies for body growth. Any evidence of a positive covariation between body growth or reproductive effort during early life and the intensity of senescence (as revealed in table 1) provides support for the disposable soma theory [11], as concluded by several authors of the compiled studies (electronic supplementary material, table S2).

This disposable soma theory proposes a comprehensive explanation of an organism's ageing processes starting at the molecular level. Basically, it posits that accurate gene replication and cell reproduction require a complex molecular machinery for error corrections to ensure proper cell functioning in time and across generations [11,13]. Because these error corrections or quality control mechanisms are energetically costly ([11,13] but see also [60] for a thorough discussion of the energetic costs of these mechanisms), individuals are expected to optimize their allocation to somatic maintenance according to their average lifespan or their risk of environmentally driven mortality [12]. Such relationships are well supported at the interspecific level where long-lived species have more efficient repair mechanisms than short-lived species (e.g. [61] and references therein). However, none of the studies we reviewed quantified simultaneously the accumulation of molecular and cellular damage caused by a given allocation to reproduction or growth and the fitness consequences of this damage accumulation.

Up to now, most studies that have investigated physiological costs of reproduction expenditure have focused on oxidative stress. The production of reactive oxygen species (ROS), such as free radicals in the mitochondria might be boosted in individuals that allocate a substantial amount of energy to reproduction or growth during early life. In addition, if most resources are diverted to reproduction or growth, it might jeopardize an individual's ability to allocate into maintenance mechanisms such as antioxidant machinery [62,63]. Overall, this imbalance in the ROS production rate could cause damage to cell structures (DNA, lipids and proteins), which will potentially lead to ageing [64]. The role of oxidative stress in mediating early-late life trade-offs is currently heavily debated (see [64,65] for recent reviews) and it appears that studies combining repeated measures of life-history traits with physiological and/or molecular measures over the whole individual life are needed. To date, only a few longitudinal studies have tested for an association between reproductive effort and oxidative damage [66,67]. For instance, lactating females suffer from higher oxidative

damage to plasmatic proteins than non-lactating females in red squirrels (*Tamiasciurus hudsonicus*) [68]. Ultimately, such studies linking the allocation of energy to body growth or reproduction with somatic damage should also test whether the accumulation of molecular damage leads to increased senescence rates. Such evidence would put the mechanistic explanation proposed by the disposable soma theory as a key factor shaping trajectories of life-history traits over individual lifetime in the wild.

(b) Antagonistic pleiotropy

Boundaries between evolutionary theories of ageing can sometimes be tenuous, as it is the case between the antagonistic pleiotropy and its physiological corollary, the disposable soma theory. Indeed, both theories share the same predictions in terms of trade-offs between reproduction and ageing [15,69,70]. The antagonistic pleiotropy can even be seen as a special case of the disposable soma theory, when some alleles code for a given resource allocation to reproduction during early life instead of a resource allocation to maintenance mechanisms later in life [14,15,71], although some alleles with antagonistic effects might involve pathways independent of somatic maintenance [72].

However, the theoretical frameworks of antagonistic pleiotropy (population genetics) and of the disposable soma theory (optimization theory) differ quite markedly [5,69]. Therefore, any simple evidence of a trade-off between body growth or reproduction early in life and fitness-related traits in late life supports the disposable soma theory [73], but not necessarily the antagonistic pleiotropy theory for which any firm test in wild populations requires a quantitative genetic approach [70]. So far, only two long-term studies of wild populations on mute swans (*Cygnus olor*) [23] and red deer [74] have properly demonstrated the genetic basis of a trade-off between allocation to reproduction during early life and fitness-related traits in late life. In addition, only studies performed on model species and humans have to date uncovered which specific genes might be involved in the relationship between the number of offspring produced in early life and performance at an advanced age. For instance, experimental genetic manipulations in mice identified six genes with antagonistic effects on life histories, involving lengthening lifespan (up to 70%) while reducing reproductive rate and delaying age at first reproduction (see [5] for a review). In humans, a specific allele of the gene coding for the apolipoprotein E (APOE*2) implicated in lipid metabolism is both negatively associated with fertility and positively associated with lifespan [75]. However, whether such genes could account for observed senescence patterns and provide support for the antagonistic pleiotropy theory in the vertebrate species, where the presence of an early-late life trade-off has been documented is still to be investigated.

(c) Principle of allocation

The Cody principle of allocation [76] states that organisms allocate acquired energy either to growth, reproduction or survival in a competitive way so that trade-offs should occur. This is at the core of our current theory of life-history evolution [77]. However, the disposable soma theory described above was initially formulated without any explicit reference to Cody's [76] work and simply aimed to explain the evolution of ageing at the cellular level, based on the assumption that errors must occur at some stage in somatic macro-molecular

synthesis over an organism's lifetime, leading to a fatal breakdown of homeostasis, and ultimately to death [11]. That the disposable soma theory was not initially framed in a life-history context probably explains why about half of the studies (10 of the 21) that reported a negative covariation between allocation to reproduction during early life and individual performance in late life have simply been interpreted as a trade-off between biological functions or life-history traits (electronic supplementary material, table S1) without any explicit reference to evolutionary theories of ageing. However, predictions of the disposable soma theory perfectly match the principle of allocation and the derived Van Noordwijk & de Jong [54] Y-model of allocation. This model does not distinguish between immediate and delayed reproductive costs, but rather states that within a population a negative covariation should occur between current reproduction and future survival, or reproduction when the individual variation in resource allocation is greater than individual variation in resource acquisition.

Recently, Baudisch & Vaupel [78] proposed that the principle of energy allocation (named 'Allocation theory' in their study) could offer a possible framework that would explain observed discrepancies between theory and data on ageing (see [3]). For instance, current evolutionary theories of ageing predict that mortality should increase steadily from the age at first reproduction [7], while empirical evidence shows that the age at onset of senescence is sometimes delayed and occurs much later [79]. This might be easily explained if the energy costs associated with a large allocation to body growth or to reproduction during the first part of life brings forward the age when reproductive or survival probabilities start to decline. Moreover, Baudisch & Vaupel [78] argue that allocation trade-offs underlying the ageing process occurs across the whole life of an organism and not only between early and late life. Overall, boundaries between the disposable soma theory and the principle of allocation remain thin even if the latter appears broader when it comes to considering the timing of trade-offs between life-history traits [78]. Studies reviewed here provide clear evidence that the ageing process is embedded in the evolution of life-history strategies and covaries with other biological processes like growth and reproduction.

4. Future directions

(a) Natal environmental conditions

It has recently been suggested that among current theories of ageing, the disposable soma theory might be the most likely to explain the diversity of ageing patterns across the tree of life [3]. This is because this theory involves a trade-off between allocation to body growth or reproduction and allocation to mechanisms that limit senescence, and the outcome of this trade-off depends on environmental conditions [12]. For instance, under a high risk of environmentally driven mortality, individuals are expected to favour allocation to reproduction over maintenance, which will ultimately influence the evolution of ageing [73]. Environmental conditions around birth can potentially alter the optimal allocation between maintenance and reproduction. Among the 26 studies, we collected that tested for a trade-off between reproduction or growth during early life and fitness-related traits in late life (table 1), only three directly assessed the effects of environmental conditions on late-life performance [22,25,30]. These studies revealed that the natal environment is associated with variation

in senescence rates. In red deer, females born in years of high population density have more rapid senescence in both survival and reproduction than females born in years of low population density ([30]; see also [80–82] for studies linking natal conditions and senescence rates in the wild). These studies [22,25,30] also provide support for an early-late life trade-off by reporting a negative correlation between allocation to reproduction in early life and performance in late life, if all individuals in the study are pooled regardless of their natal conditions.

At the same time, there is also evidence that natal conditions can have antagonistic effects on fitness-associated traits in early and late life. In Mauritius kestrels (*Falco punctatus*), females born in habitats modified by agriculture recruit more fledglings during early adulthood than females born in habitats without agriculture, whereas the opposite relationship is observed when females are older than 6 years of age [83]. Interestingly, such differences in age-specific recruitment do not influence female lifetime reproductive success, suggesting that habitat heterogeneity leads to the coexistence of different life-history strategies [83]. Early conditions experienced by individuals might be used as a cue of future somatic state. In such cases, the so-called internal predictive adaptive response (PAR) assumes that individuals born in poor-quality environments should anticipate and respond to their future poor body condition and associated risk of dying prematurely by early maturation [84]. More generally, animals could increase the energy allocation to early reproduction in situations where a poor start in life is associated with an accelerated senescence in survival or reproductive performance. In such cases, contrary to both disposable soma and principle of allocation theories, the reduced longevity or increased senescence is not a consequence of a greater allocation to reproduction or growth early in life, but rather corresponds to a direct effect of adverse natal conditions. Direct tests of the internal PAR hypothesis are currently lacking in wild populations but again would provide important insights regarding the links between the quality of the natal environment and life-history trade-offs. Overall, testing predictions about life-history responses to environmental variability may provide a step further towards an integrated life-history theory of ageing underpinned by the set of physiological or genetic mechanisms offered by the disposable soma and the antagonistic pleiotropy theories.

(b) Sex-differences in ageing patterns

Our review highlights that studies investigating early-late life trade-offs are generally focused on females. However, comparing long-term costs of allocation to growth and reproduction on both males and females within a given species would allow understanding of the origins of sex-differences in senescence patterns, which is currently a central question in evolutionary biology (see [85–87] for recent reviews). It is now well known that males and females differ in longevity in most wild populations of vertebrates (e.g. in mammals, females typically outlive males, whereas the opposite is often found in birds; [88]), a difference that is also observed in terms of senescence rates. For example, in free-ranging ungulates, males suffer from a much steeper rate of senescence than females [89]. Such differences have been mainly interpreted as a consequence of sexual selection, with costs associated with polygynous mating systems causing faster senescence in males than in females ([85–87,90]; but see [91]). Indeed, defending a group

of females or a territory during the breeding season is responsible for substantial energetic costs in males of polygynous species (e.g. [92,93] for examples of body mass loss during the mating season). So far, the influence of sexual competition and mating tactic on survival and senescence patterns has been principally analysed across species [89,94]. Such trade-offs were rarely investigated on a within species level, maybe because pioneering works in evolutionary ecology of ageing did not explicitly mention sexual selection [10–12]. However, there is increasing evidence that higher male allocation to sexual competition during early life accelerates senescence. This is well illustrated by the polygynous red deer in which males with the largest harems between 4 and 9 years of age have much steeper senescence rates in harem size and number of days spent rutting once they reach 10 years old [32]. More studies of contrasting male reproductive tactics and allocation to secondary sexual traits, which markedly differ across species [95] are now required to understand how the intensity of sexual competition influences senescence patterns.

It is also of utmost importance to investigate the role of sexual selection in shaping variation in senescence simultaneously in both sexes within a given species. There is a long-standing interest in evolutionary ecology in quantifying the physiological costs of long periods of reproductive activities in females (e.g. gestation, lactation or incubation costs), particularly those assumed to be strongly energy demanding (e.g. [96] for birds or [97] for mammals). However, how sex-specific costs of reproductive allocation shape sex-differences in ageing trajectories and thereby modulate evolutionary and demographic processes in return has yet to be investigated. A first step in that direction has recently been achieved by Rubolini and colleagues who reported higher levels of oxidative damage to plasma proteins during the pre-laying period in females than in males in barn swallows (*Hirundo rustica*) [98]. Whether such sex-differences in physiology translate into senescence patterns or longevity remains unknown. Investigating such questions in the wild where variable environmental conditions influence both the direction and

intensity of sexual competition [99] constitutes an exciting opportunity to understand variation in senescence rates across populations.

5. Concluding remarks

The empirical evidence we reviewed strongly supports that high allocation to reproduction or growth early in life is associated with earlier or faster senescence late in life, in accordance with the general principle of allocation. This thereby provides support for the disposable soma theory, and potentially for the antagonistic pleiotropy theory, if genes involved in such trade-offs are identified. Our review indicates that the process of senescence should be interpreted in the broad context of life-history evolution and should contribute to the emergence of a more integrative principle of allocation. We particularly highlight the importance of considering energy allocation and differential trade-offs in both sexes, in addition to how fluctuating environmental conditions explain the diversity of ageing in the wild. Further examination of these questions will open new paths for future investigations.

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Endnote

¹For the sake of simplicity, the terms *senescence* and *ageing* will be considered as synonymous.

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