



The effects of reproduction on senescence in breeding birds



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Abstract

Declining survival and reproduction are part of life history. The decline of fitness components with age is called senescence and can be measured as actuarial senescence and as reproductive senescence. Due to high extrinsic mortality senescence was thought not to happen in wild populations, although lately many studies have shown that senescence does occur in wild populations. The disposable soma theory and antagonistic pleiotropy theory both predict trade-offs between current reproductive investment, and survival and reproduction later in life. Experimental studies have showed that increased reproductive effort leads to accelerated senescence. In this thesis I will compare the relationship between and within longer and shorter living bird species. Longer and shorter living birds adopt very different reproductive strategies. Shorter living birds invest more in early life reproduction while longer living birds invest less in reproduction and more in somatic maintenance. Senescence due to reproduction eventually does occur in longer living species but at a much older age because of their low reproductive investment and high investment in maintenance. Within species these differences also arise, with some individuals investing more in reproduction also senesce faster, although some studies also found that high quality individuals do not seem to face costs of reproduction in terms of accelerated senescence. I also compare the impact of reproduction on senescence between males and females. In mammals male biased mortality is very general, however, male biased senescence is not as obvious in birds because of lower male-male competition, increased female biased senescence due to parental care and because the female is the heterogametic sex which is associated with higher mortality due to deleterious mutations on the sex chromosomes. Finally, I will explain how it may be possible that birds generally live longer than mammals in terms of protection against oxidative stress and I will discuss if the effects of reproduction on oxidative stress can be measured via telomere shortening. Overall, these findings support the disposable soma theory which states that higher investment in reproduction leads to accelerated senescence, however, the antagonistic pleiotropy theory cannot be excluded which emphasizes the need for more genetic based research.

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Introduction

Declines in survival and reproductive performance are part of the life history in many species. (Jones et al., 2008). Senescence is the decline in fitness components with age (Lemaitre et al., 2015). There are different theories about the evolution of senescence. The disposable soma theory and the antagonistic pleiotropy both assume that senescence can evolve because natural selection weakens with age because it is proportional to the number of individuals still alive in different age classes.

The disposable soma hypothesis of senescence states that successful life history strategies require resources to be allocated from maintenance and repair to growth and reproduction (T. B. L. Kirkwood & Rose, 1991). Resources are usually limited and therefore individuals must divide them among growth, maintenance and reproduction. High mortality is associated with a rapid decline in the force of selection with age. Therefore, animals exposed to high extrinsic mortality, for example by predation, should invest heavily in high early-life reproduction while individuals exposed to low extrinsic mortality should invest in their own survival to create multiple breeding opportunities.

Antagonistic pleiotropy theory also predicts a trade-off between survival and reproduction. This theory is different because it is a genetic-based theory. It states that some alleles improve reproduction in early life at the cost of maintenance later in life. Here, senescence may be caused by weaker selection on late-acting deleterious mutations. This leads to greater selection on genes that are beneficial during early life, but have deleterious later life effects (Williams, 1957).

Any evidence for a trade-off between growth, maintenance or reproduction early in life and fitness related traits in late life supports the disposable soma theory, but is not necessarily direct evidence for the antagonistic pleiotropy theory, as testing that theory requires a quantitative genetic approach (Lemaitre et al., 2015). It is, however, generally considered that both theories lead to similar predictions in terms of life history trade-offs between investment in reproduction during early life and

intensity of ageing in late life (T. B. L. Kirkwood & Rose, 1991).

Individuals in the wild often experience extrinsic mortality, which causes them to die before the age in which senescence would occur is reached. However, lately many studies have shown that senescence is common in wild populations. Senescence can be measured as actuarial senescence (the increase in mortality rate with age) but a lot of biologists acknowledge that senescence can also occur in reproduction (Jones et al., 2008). Therefore, not only a trade-off may occur between early-life reproduction and survival but also between early-life and late-life reproduction.

In wild vertebrates there is a lot of variation in senescence rates (Jones et al., 2008).

Birds senesce slower than mammals due to their slower life history for a given body size (Holmes & Austad, 1995). Also, birds display many different reproductive strategies and mating systems which makes them especially interesting to study long term effects of reproduction on senescence.

In this literature study, I will first compare the relationship between reproduction and senescence between and within longer and shorter living bird species. Second, I will compare the impact of reproduction on senescence between males in females in monogamous (females and males only mate with each other) and polygynous (males mate with multiple females while females only mate with one male) mating systems and compare the differences in sex-biased effects between mammals and birds. At last, I will explain how it may be possible that birds live longer compared to mammals in terms of protection against oxidative stress and I will discuss if the effects of reproduction on oxidative stress can be measured via telomere shortening. Finally I will discuss the different results in effects of reproduction on senescence and I will discuss the further need for research combining genetics and environmental/individual condition in wild populations.

Actuarial senescence between and within species

Actuarial senescence (the increase in mortality rate with age) is thought to arise through the accumulation of somatic damage, which makes organisms more susceptible to environmental and physiological challenges (T. B. L. Kirkwood & Rose, 1991).

Populations exposed to higher mortality from extrinsic factors (e.g. accidents predation) are expected to mature faster, show higher early-life reproductive investment and higher fecundity. On the contrary, when mortality risk is lower, natural selection should favor individuals with slow aging rates and adaptations that ensure somatic maintenance (Thomas B L Kirkwood & Austad, 2000).

According to life-history theory, species should adopt the reproductive strategy that results in the highest lifetime fitness. If reproductive effort in one year results in a loss of future reproductive success, then the optimal effort in the current season is less than the investment that would maximize the number of offspring in that season (Charnov & Krebs, 1974).

Species not subjected to high mortality may have multiple breeding attempts and should therefore not invest too heavily in reproduction when this jeopardizes the chance of breeding again due to a higher mortality probability. Shorter-living species, on the other hand, should invest heavily in early reproduction because they might not get multiple breeding opportunities.

Indeed, longer- and shorter-living species show very different reproductive strategies.

Generally, longer living species mature later and display a later onset of first breeding attempt compared to shorter living species. A later onset of first breeding correlates positively with lifespan in longer living species. Shorter living species, on the contrary, mature more quickly, and attempt to breed at a younger age (Mourocq et al., 2016).

Also longer living species may choose not to breed every breeding season when conditions are unfavorable and wait for better breeding opportunities. For example, in the Florida Snail

Kite (*Rostrhamus sociabilis plumbeus*), there is a significant decline in proportion of adults that try to breed during drought years (Reichert et al., 2018).

An example of very long living birds are albatrosses and petrels that belong to the order Procellariiformes. These species are unique in their reproductive strategy. They lay one egg every breeding attempt and their maturity is delayed up to 13 years. They can live up to 65 years and are somewhat homogenous in their pelagic lifestyle. Some individuals travel up to thousands of kilometers during the breeding season. Despite their very slow reproductive strategy these birds also show significant trade-offs between reproduction and survival. Birds that produced more eggs or produced more chicks per year showed significantly lower survival. This suggests that long living species must reduce the investment in reproduction to maintain higher survival rates (Dobson & Jouventin, 2010).

The weakness of this study in Procellariiformes is, however, that it is an interspecific approach which makes it impossible to directly measure causal effects. The solution for this is to experimentally manipulate reproductive effort. A recent study finds that Jackdaw (*Coloeus monedula*) parents raising experimentally enlarged broods for multiple years had a threefold higher probability to die compared to parents raising reduced broods (figure 1) (Boonekamp et al., 2014).

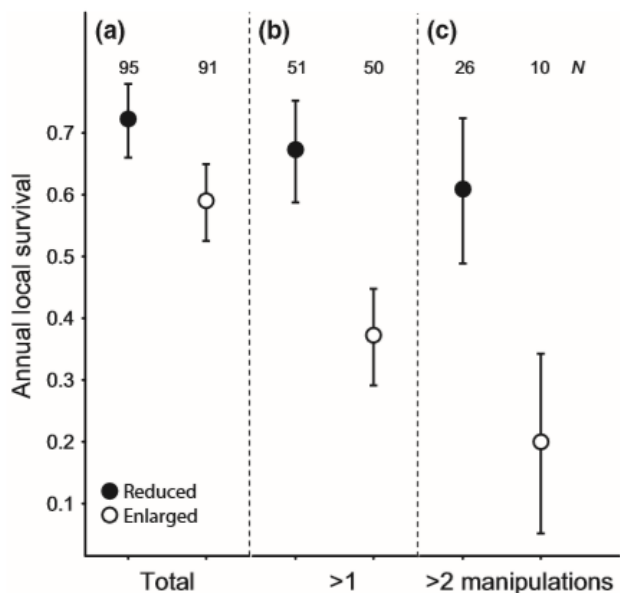


Figure 1. Mean annual local survival rate of parents rearing enlarged or reduced broods. Y-axis represents the probability to return corrected for the probability of recapture. Total on the X-axis refers to data of all individuals, >1 to individuals receiving more than 1 brood size manipulations. >2 refers to individuals that received more than 2 brood size manipulations (Boonekamp et al., 2014).

These effects may even be an underestimation of the impact of reproduction since it does not account for the costs associated with egg production and incubation (de Heij, van den Hout, & Tinbergen, 2006).

Another study in red-billed choughs (*Pyrrhocorax pyrrhocorax*) found that within a population longer living parents produced offspring that was less likely to survive the first year than offspring from shorter living parents. This negative correlation was strongest when environmental conditions were less favorable, thus suggesting an environmental-dependent trade-off between parent and offspring survival (Reid et al., 2018).

Overall, these findings support the disposable soma theory: resources used for reproduction can no longer be used for somatic repair and the accumulation of somatic damage makes the individual more vulnerable to physiological and environmental damage, which results in accelerated actuarial senescence.

Reproductive improvement, senescence and carry-over effects

In the wild there is only a limited amount of resources available, thus individuals can only acquire a limited amount of energy. Reproduction and survival, but also current and future reproduction, are thought to be functions competing for the same resources. Life history theory thus predicts a trade-off between early and late reproduction (Lemaitre et al., 2015).

Reproduction, however, does not necessarily affect future reproduction negatively. In many bird species, reproductive output first increases with age before it decreases. A hypothesis that has been proposed to explain this phenomenon is that breeders become more effective in their resource acquisition when they gain breeding experience (Curio 1983). Alternatively, according to the selection and recruitment hypothesis high quality individuals perform well in reproduction and survival while low quality individuals die sooner and reproduce less well. This creates an age-related decrease of proportion of lower-quality individuals in cohorts (Forslund & Pärt, 1995). To distinguish effects on population level and effects that occur at the level of the individual one must track individuals to determine reproductive success over multiple breeding years. So far, research has found proof for both explanations. In Leach's storm petrels (*Oceanodroma leucorhoa*) (a long living seabird) there was a strong positive correlation between breeding success in the first two breeding attempts and longevity. This suggest that parents with low reproductive success also were less likely to survive early breeding attempts and this thus provides support for the selection hypothesis (Mauck et al., 2004).

A study on Seychelles Warblers (*Acrocephalus sechellensis*) found some evidence for the breeding experience hypothesis. The Seychelles Warbler is a cooperatively breeding bird, which means that birds can breed for themselves but they can also help others with breeding. Translocation of unexperienced birds and non-breeding helpers of the same age showed that birds that had previous helping experience

produced their first fledgling faster than unexperienced first breeders and as fast as experienced breeders. This showed that helpers gained breeding experience, which resulted in higher reproductive success when they started breeding for themselves (Komdeur, 1996).

A study on Common blackbirds (*Turdus merula*) found that both selection and learning resulted in increasing reproductive success with age. Although reproductive success decreased again at older age (Jankowiak, Zyskowski, & Wysocki, 2018).

In tree swallows (*Tachycineta bicolor*), reproductive success increased with age, but not with breeding experience. Experienced individuals of the same age did not perform better than unexperienced individuals but they did perform better than younger animals. Also older unexperienced individuals performed better than younger experienced individuals in terms of reproductive success. Since there was no improvement in breeding effort with experience (laying date, clutch size, feeding rate, incubation efficiency), these results suggest an age-related improvement which may be caused by other skills devoted to maintenance like feeding (Robertsen & Rendell, 2009).

So reproductive success can, at first, increase due to acquired breeding skills or skills devoted to maintenance but it is also possible that for some species there is an apparent improvement in reproductive success at population level in older animals due to selective mortality of lower-quality individuals, which results in an age-related decrease of proportion of lower-quality individuals in cohorts.

Although reproductive success at first increases in many bird species, several studies show that the oldest cohorts eventually show a reproductive decrease.

In Seychelles warblers senescence does occur at older age. Reproductive success increases from age two till five, but after that it decreases again (Komdeur 1996a).

A study in guillemots (*Cephus grylle*) found that in the last 3 years before death individuals showed declines in reproductive success. Older birds were less likely to hold a breeding site, showed fewer attempts to breed and were less

likely to raise a chick. The rate of senescence was associated with higher levels of early-life reproductive effort.

Guillemots investing heavily in early-life reproduction had reduced reproductive success in late life suggesting a trade-off between current and future reproduction (figure 2) (Reed et al., 2008).

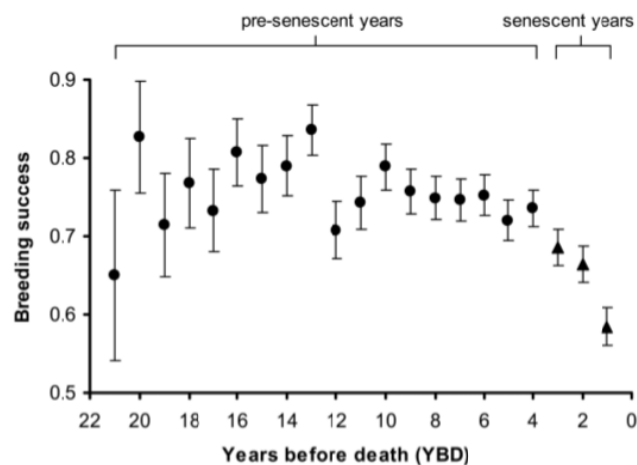


Figure 2. Breeding success measured as the proportion of events where a chick was raised to depart the colony and the relationship with years before death. Data points represent individuals. Triangles represent senescent years and circles the presenescent years. In senescent years breeding success was significantly lower than in presenescent years (0.646 ± 0.018 vs 0.744 ± 0.001 ; $X^2=21.55$, $df=1$, $P<0.001$) (Reed et al. 2008).

Similar results were found in Great tits (*Parus major*). Fledgling production in early life was related to accelerated reproductive senescence (Bouwhuis et al., 2018).

Reproductive senescence at older age may be caused by hormonal change. Multiple studies found that several hormonal levels changed with age in both males and females (Cabezas-Díaz, Virgós, & Villafuerte, 2005)(Wilcoxon, Bridge, Boughton, Hahn, & Schoech, 2013). Also, condition dependent traits may be affected in older birds, in barn swallows (*Hirundo rustica*) the length of outermost tail feathers decreased with age (Møller & De Lope, 1999).

Reductions in reproductive success as a result of increased current reproductive effort do not only occur at older age. There is also evidence showing trade-offs between breeding seasons. Sexual displays like ornaments require energy, affect fitness, and should therefore be regarded

as life history traits (D. E. L. Promislow, Montgomerie, & Martin, 1992). Increased energy allocation to reproduction should thus lead to a decreased elaboration of ornaments in in subsequent breeding years. Research on eastern bluebirds (*Sialia sialis*) showed that males rearing reduced broods had brighter plumage next breeding year,. Brighter plumage is considered as an honest signal of male condition in this species and males with brighter plumage are more likely to obtain a high quality female and have greater reproductive success (Siefferman & Hill, 2005). In great tits, reproductive effort also correlated negatively with future competitive ability. Parents raising enlarged broods were less likely to obtain a scarce high-quality breeding site in the subsequent breeding season (Fokkema, Ubels, & Tinbergen, 2016). These findings confirm carry-over effects of reproduction between subsequent breeding years.

In conclusion, many birds first show an increase in reproductive success with age, which may be caused by gained experience devoted to breeding or maintenance, but also by selection resulting in an age-related decrease of proportion of lower quality individuals in cohorts. Also, energy invested in one breeding season may affect the next season via carry-over effects. Senescence, however, does seem to occur at older age in many birds and can arise through hormonal change or lower body condition and can be accelerated by high investment in early life reproduction, thus supporting the disposable soma hypothesis.

Non male biased senescence in birds

Typically, adult human males have a lower life expectancy compared to females, which is associated with an earlier onset and a faster progression of senescence in males than females. In western societies, where humans have access to abundant resources males show earlier senescence and lower life expectancies than females (Austad, 2006). This trend is also observed in many mammals (Daniel E L Promislow, Proceedings, Sciences, & Mar, 2016).

Both antagonistic pleiotropy and disposable soma theory predict that the sex with the higher rate of mortality will suffer faster senescence because selection for increased investment in early reproduction over somatic repair will be stronger in this sex with negative effects on late life vitality (Williams, 1957).

A possible explanation for the evolution of earlier senescence in males than females is more intense intrasexual competition for breeding opportunities combined with costs associated with traits or strategies that enhance competitive success, which shorten the period in which males are able to attract or defend females against competitors. Selection favoring longevity will therefore be weaker in males (T. B. L. Kirkwood & Rose, 1991).

If competition affects longevity one would expect higher male biased senescence in polygynous mating birds where males mate with multiple females and experience high competition levels, compared to monogamous mating birds where males and females only mate with each other.

A comparative study found that in vertebrate polygynous species male survival was indeed lower compared to females. Males in polygynous mating systems had lower annual survival probability and increased senescence at the end of their lifespan. Contrarily, sex biased senescence differences and differences in life expectancy were smaller and less consistent in monogamous species (Clutton-Brock & Isvaran, 2007).

Higher senescence rates in polygynous species are probably caused by greater reproductive benefits of winning encounters for males and traits that increase competitive success are usually traded-off against survival (Clutton-Brock & Isvaran, 2007).

Although this seems convincing, most polygynous species in this research were mammals. There were only three polygynous bird species, which gave mixed results. In red winged blackbirds (*Agelaius phoeniceus*), a polygynous species, males do not show increased senescence compared to females. This could be because this is a relatively short living species. In the longer living tetraonids (e.g.

partridges and grouses) also a polygynous species, males showed increased senescence compared to females. Suggesting that competition effects on senescence maybe only show in longer living species because they have accumulating effects which do not show in short living species due to high extrinsic mortality. Other research also did not find evidence for male biased mortality in birds in monogamous mating systems, instead the female is often the one with slightly higher mortality rates (D. E. L. Promislow et al., 1992).

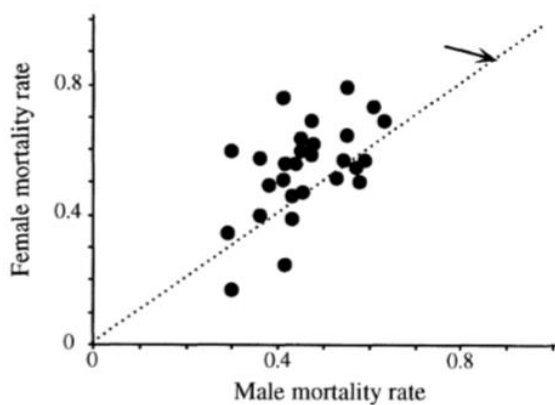


Figure 3. Adult female mortality against adult male mortality in 28 North American passerine species. Female mortality was higher in 21 species. Line indicates equality (Promislow et al., 1992).

So how does higher female-biased senescence arise. Parental care theory predicts a higher mortality in the sex that invests most in parental care like incubating and raising young, which is often the female. Parental care often affects mortality and especially post-hatching components of care like provisioning food and brood defense seem costly (Owens & Bennet, 2018). Passive brood defense is associated with higher mortality rate than active brood defense. This may explain why there is female biased mortality in species that use this strategy since females often brood more and thus experience high predation whilst brooding (Owens et al., 2018).

Also, birds differ from mammals because the female is the heterogametic sex (females ZW, males ZZ) whereas in mammals the male is the heterogametic sex. Thus, female birds are more vulnerable to mutations on the Z chromosome. Most deleterious mutations tend to be recessive

thus these alleles are more exposed to selection in the heterogametic sex. Also the Z chromosome is bigger than the W chromosome, so there are probably more possibilities for mutations in the Z chromosome. Therefore the heterogametic sex, thus in birds the female, is expected to have higher mortality (Liker & Szkely, 2016).

In conclusion, bird populations often don't show male biased mortality because birds are mostly monogamous and males thus experience less intense male-male competition, also females experience more mortality due to parental care like brooding and because females are more likely to suffer from deleterious mutations.

Oxidative stress and reproduction in birds

Oxidative stress is considered as an important cause of senescence (Finkel & Holbrook, 2000). During oxidative metabolism, mitochondria generate unstable reactive oxygen species (ROS). ROS can cause damage because they interrupt redox signaling/control and can cause molecular damage in for example DNA, RNA, proteins and lipids (Storz & Imlay, 1999). Oxidative stress is the balance between exposure to and protection against ROS by, for example, antioxidants.

The rate of living theory predicts that life spans are constrained by their metabolic rates and resulting cellular wear and tear. This theory is based on the strong positive correlation between body size and maximum lifespan within vertebrate classes and a negative correlation between species lifespans and basic metabolic rates (Pearl 1928).

An expansion of this theory is the free-radical and oxidative damage theory about ageing that predict that organisms with high metabolic rates and lifetime oxygen expenditures produce higher rates of ROS (Harman 1956).

Via a variety of pathways, ROS could negatively affect reproduction and survival because it causes apoptosis (programmed cell death), proliferation (rapid cell production), growth arrest and senescence. Animals with high metabolic rates thus produce more ROS because

of higher oxidative metabolism and senescence faster as a result of this. Birds live relatively long despite having high metabolic rates and high lifetime oxygen expenditures, which makes them very interesting for research on senescence in terms of oxidative damage. Several existing mechanisms have been suggested as possible explanations for reducing oxidative damage in bird species. Some of which include better defense against ROS, like decreased levels of fatty acid unsaturation in mitochondrial membranes (Hulbert et al., 2007) or increased levels of antioxidants (Torres & Velando, 2007). Other explanations include evidence that avian mitochondria may produce less ROS during oxidative metabolism and thus creates less cellular damage in the first place (Barja et al., 1994). Since oxidative stress is thought to be one of the major candidates for causing senescence, one might wonder if reproduction affects senescence through increasing oxidative stress. Oxidative stress due to resource allocation towards reproduction has been suggested to be an important mechanism underlying the trade-off between reproduction and senescence. Evidence in bird species is scarce but some studies found that senescence via protection against oxidative stress can, at least partially, be influenced by reproduction. Brood size manipulations in zebra finches (*Taeniopygia guttata*) showed that parents with enlarged broods showed reduced antioxidant levels. This suggests that reproduction affects protection against ROS, which eventually may lead to accelerated senescence (Alonso-Alvarez et al., 2004)(Wiersma et al., 2004). Self-maintenance and future reproduction is also expected to be more important than current reproduction in longer living birds species. Adélie penguins (*Pygoscelis adeliae*) experiencing increased breeding constraints also increased their antioxidant capacity, suggesting these longer living birds also prioritize self-maintenance and possible future reproduction (Beaulieu et al., 2011). These findings suggest that reproduction may lead to increased levels of ROS which can be measured in defense mechanisms like antioxidants. The reactions, however, differ between species and

may be a reflection of longevity but further research is required to conduct conclusions.

Telomeres as biomarker of senescence

Biomarkers of senescence are important when predicting mortality and age-related diseases. Telomeres are non-coding sequences at the end of chromosomes that protect DNA during cell division (Armanios & Blackburn, 2012). Telomere length declines in somatic cells due to incomplete replication during cell divisions. Older mammals and birds typically have shorter telomeres although there is great variation within age groups which may have a genetic basis but can also be caused by life style and associated stress (Atema et al., 2015). Telomeres may shorten by reproduction because of its effect on oxidative stress. ROS could damage cells and accelerate cell divisions which cause further telomere loss (Von Zglinicki, 2002). Telomere length could therefore be considered more as a marker of biological senescence rather than age.

Reproductive effort has negative effects on telomeres. For example, in migratory birds arrival date is associated with telomere shortening, but also laying date, clutch size and reproductive success have been associated with shorter telomere lengths, independent of actual age (Bauch, Becker, & Verhulst, 2012). High investment in reproduction leads to greater reproductive success but probably at the expense of telomere length, which eventually may lead to a shorter lifespan. Contrarily, the study in Adélie penguins mentioned before did not find effects of reproduction on telomere shortening (Beaulieu et al., 2011). Because Adélie penguins up-regulate their antioxidant defense they may have protected their telomeres against ROS.

Another study found that initial telomere length differed between sexes and decreased with age which also depended on environmental quality (Young et al., 2013).

Thus, telomere length change may be considered as a reflection of biological age or senescence since telomere lengths are partly

independent of age and highly variable within species due to a genetic basis and lifestyle-associated oxidative stress, for example by reproduction. However, some species may have evolved ways of limiting effects of oxidative stress on telomeres and environmental quality may affect change in telomere length which makes telomeres possibly not the best way to assess costs associated reproduction in avian species.

Discussion

Despite high extrinsic mortality many studies found that senescence is likely to occur in wild populations. The disposable soma theory predicts that high investment in reproduction should lead to accelerated senescence because resources are no longer allocated to maintenance and repair (Thomas B.L. Kirkwood, 2002). This can be measured as actuarial and reproductive senescence (Jones et al., 2008).

In this literature study I found that longer and shorter living species have very different reproductive strategies with shorter living species investing more in current reproduction while longer living species invest more in maintenance.

When extrinsic mortality is high it is less advantageous to invest in maintenance and more advantageous to invest in early reproduction, and vice versa.

Different lifespans do not seem to be a direct cost of reproduction but rather an adaptive reproductive strategy because selection acts in different directions favoring investment in reproduction in shorter living species and maintenance and slow breeding in longer living species (Mourocq et al., 2016). Disposable soma theory may therefore be the major candidate in the evolution of longevity driven by the level of extrinsic mortality (T. B. L. Kirkwood & Rose, 1991).

Within species the trade-off between reproduction and senescence is also visible, individuals investing more in reproduction do show accelerated actuarial and reproductive senescence (Dobson & Jouventin, 2010)(Reid et

al., 2018). Individual variation in quality can, however, mask the effects of reproduction since some high quality individuals do not only reproduce more but also survive better, which supports the selection hypothesis that predicts an age-related decrease of proportion of lower quality individuals in cohorts (Mauck et al., 2004). One can wonder if the oldest cohorts in natural populations are therefore a good representation of senescence in older birds. These findings emphasizes the need for experiment with enlarged or reduced clutch or brood size since it can minimize effects of natural variation (Boonekamp et al., 2014). Also, environmental conditions may induce a larger or smaller cost of reproduction (Fay et al., 2018)(Nevoux et al., 2008) and can even lead to skipping of breeding seasons (Reichert et al., 2018).

Oxidative stress is a likely mechanism underlying the costs of reproductive investment, although reactions in defense mechanisms like antioxidants are very different with some species becoming more vulnerable while others upregulate their antioxidant levels, this may depend on lifespan but more research is required to conduct conclusions (Alonso-Alvarez et al., 2004)(Beaulieu et al., 2011)(Wiersma et al., 2004). Also, telomere shortening may not be the best way to assess costs of reproduction since antioxidant defence mechanisms limit the damaging effects of ROS on telomeres and effects are influenced by environmental conditions (Beaulieu et al., 2011)(Young et al., 2013).

Antagonistic pleiotropy theory and disposable soma theory both predict the same trade-offs in terms of reproduction and senescence but the underlying mechanism is very different. Antagonistic pleiotropy theory predicts that senescence occurs due to selection on genes that are beneficial during early life, but have deleterious effects later in life. Several studies confirmed antagonistic pleiotropy in fruit flies (*Drosophila melanogaster*) (Luckinbill et al 1984), red deer (*Cervus elaphus*) (Nussey et al) and also in mute swans (*Cygnus olor*).

In this literature study I found evidence which strongly support that high allocation to early life

reproduction is associated with accelerated senescence. Most research in this literature study support the disposable soma hypothesis but the antagonistic pleiotropy theory cannot be excluded since they predict the same trade-offs. Also, there is broad evidence that senescence as a consequence of reproduction depends on individual quality and environmental conditions. I suggest that these findings emphasize the need for more research linking genetics, environmental/individual conditions and senescence rates in wild populations.

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