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Rethinking the Evolution of Ageing: From Mutation Accumulation to Social Transfers and Negligible Senescence

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ABSTRACT

The theory of aging explains why death becomes more common as individuals grow older. It suggests that as we age, the remaining years available for repro- duction decrease, making our survival less important for passing on our genes. However, with recent developments, it has been observed that general theories do not adequately account for the lives of social animals. Successful reproduction in these animals involves not only having children but also providing support to them and other younger individuals. Over time, several theories have been devel- oped to combine the effects of fertility and support in determining mortality at different ages. For species that strike the right balance between producing many offspring and investing in each one, the factor of support becomes more influen- tial in mortality. By integrating transfers with fertility-based selection, a formal theory has been developed that aligns with data and applies to understanding life histories and population dynamics. This review also highlights how social insects do not conform to classical theories of aging and emphasizes the need to consider recent models of aging theories that address this limitation.

Keywords: *Evolution of Ageing, Social Insects, Longevity, Intergenerational Transfers.*

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1 Introduction

Aging, an inevitable biological process, has long fascinated scientists seeking to unravel its mysteries and understand why death becomes increasingly prevalent as individuals grow older. Various theories have been proposed to explain this phenomenon, shedding light on the intricate relationship between reproduction, mortality, and the passing on of genetic material [1, 2]. Among these theories, one intriguing concept posits that as individuals age, their remaining years for reproduction decrease, diminishing the significance of their own survival in terms of propagating their genes. This perspective emphasizes the delicate balance between producing offspring and investing in their support—a balance that influences mortality rates at different ages [3].

In recent years, an emerging theoretical framework has sought to address the limita- tions of classical theories of aging by incorporating the critical role of intergenerational transfers and support in successful reproduction and post-reproductive survival [4]. This theory recognizes that reproductive success not only involves the act of having children but also encompasses the provision of care, food, and protection to offspring and even other younger individuals within a population. By integrating fertility-based selection with the significance of transfers within social systems, this theory offers a more comprehensive framework that better aligns with empirical data and facilitates a deeper understanding of life histories and population dynamics.

Interestingly, the conventional theories of aging do not adequately account for the remarkable characteristics observed in eusocial insects. These insect societies defy the expectations set forth by classical theories, prompting researchers to explore alterna- tive explanations that consider the unique dynamics of these complex social systems [5, 6]. For instance, queens of ants and bees often live extraordinarily long lives com- pared to their worker counterparts, despite the shared genome. By examining such social insects, researchers have gained valuable insights into the mechanisms underlying aging, challenging established paradigms and highlighting the need for theories that incorporate both social behavior and evolutionary pressures.

Moreover, beyond the realm of insect societies, investigations into the impact of biomedical interventions on lifespan have yielded intriguing results. One such inter- vention, the use of the drug Rapamycin, has shown promise in enhancing longevity in a variety of organisms, ranging from yeast to mice [7, 8]. Exploring the effects of Rapamycin in humans, particularly its potential for improving both lifespan and healthspan, holds significant implications for understanding the underlying mech- anisms of aging and developing interventions that promote healthy and extended life. In this paper, we aim to present a comprehensive review of the theory that inte- grates fertility and support as fundamental factors influencing mortality and aging. We will first discuss the limitations of classical theories of aging, followed by an examina- tion of the unique characteristics of social insects that challenge existing frameworks. Finally, we will explore the potential of biomedical interventions such as Rapamycin in extending human lifespan. By combining insights from evolutionary biology, population dynamics, and biogerontology, we seek to contribute to a deeper understanding of aging and mortality, offering a unified perspective that sheds new light on this fundamental aspect of life.

2 Theories of Ageing

2.1 Classical Theories of Ageing

The foundation of evolutionary theories of ageing rests on the idea that the strength, or "force," of natural selection declines with age. This means that mutations which manifest early in life exert stronger effects on fitness than those expressed later. Because extrinsic mortality ensures a higher abundance of younger individuals, natural selection acts more strongly on traits influencing survival and reproduction early in life. This framework was first formalized mathematically by Hamilton in his pioneering work *The moulding of senescence by natural selection* [3].

Building upon earlier contributions by Fisher and Medawar, and later expanded by Williams and Charlesworth, three influential theories have dominated the field. Medawar's mutation accumulation theory emphasizes that deleterious mutations affecting late life are weakly selected against and therefore accumulate in populations over time [1]. Williams' antagonistic pleiotropy theory highlights the possibility that some mutations can be beneficial in youth but detrimental in old age, with natural selection favoring such mutations because of their early-life reproductive benefits [2, 9]. Finally, Kirkwood's disposable soma theory builds on this trade-off framework by proposing that organisms face limited resources which must be allocated between reproduction and somatic maintenance. Natural selection tends to prioritize reproduction over repair, thereby favoring higher fecundity at the cost of longevity [10].

A comparative summary of these theories is presented in Table 1.

Table 1 Summary of classical evolutionary theories of ageing.

Theory	**Core Idea**	**Implication for Ageing**
Mutation Accumulation (MA)	Late-acting deleterious accumulate due to weak selection.	Ageing arises because late-life survival and fertility matter less for fitness.
Antagonistic Pleiotropy (AP)	Mutations with early-life benefits but late-life costs can be selected.	Ageing is an unavoidable byproduct of selection for traits enhancing early reproduction.
Disposable Soma (DS)	Limited resources must be split between reproduction and repair.	Longevity is sacrificed in favor of higher reproductive success.

These theories have been instrumental in shaping the evolutionary perspective of ageing, particularly in solitary species. However, their application to cooperative and eusocial organisms reveals important limitations.

2.2 Limitations in Social Insects

Social insects, such as ants, bees, and termites, provide a striking challenge to clas- sical theories because queens and workers, despite sharing the same genome, exhibit dramatically different lifespans. Queens may live decades, while workers of the same species live only weeks or months [11]. While lower extrinsic mortality for queens partially explains this divergence, it cannot account for the magnitude of difference observed.

Kramer and Schaible [12] argue that classical frameworks fail in social insects for four main reasons. First, social insect colonies are not merely age-structured but also organized by caste and task, meaning that selection pressures differ dramatically within a colony. Second, fitness is not determined by individual reproductive out- put but rather by total colony success, where trade-offs operate at the colony level rather than the individual level. Third, workers often have no direct reproduction, but instead gain fitness indirectly by aiding the queen, highlighting the importance of inclusive fitness. Fourth, because queens and workers share overlapping genetic regulatory networks, selection acting on one caste inevitably constrains the other.

The contrast between predictions of classical theories and the reality of social insects is summarized in Table 2.

Table 2 Application of classical ageing theories to social insects.

Theory	Prediction from Classical Frame-work	Observation in Social Insects
Mutation Accumulation (MA)	Late-life mutations accumulate, reducing lifespan similarly across individuals.	Queens live decades while workers live weeks, despite shared genomes. Divergence suggests caste-specific regulation.
Antagonistic Pleiotropy (AP)	Early-life beneficial traits persist even if costly later.	Can only be applied if pleiotropic effects act across castes (beneficial to queens, detrimental to workers), rather than within a single caste.
Disposable Soma (DS)	Trade-offs limit organisms to either high fecundity or long life, but not both.	Queens display both exceptional longevity and high fecundity, as resource transfers from workers liberate them from trade-offs.

Keller [11] further demonstrated that reproductive strategy influences queen longevity. Queens in monogynous species, with only one queen per colony, tend to live longer than those in polygynous colonies, suggesting that reproductive role and colony organization are central to the evolution of lifespan. These insights show that classical models cannot fully account for the biology of social insects, requiring modifications that incorporate inclusive fitness, cooperative brood care, and colony-level trade-offs.

2.3. Broader Insights from Model Organisms

Beyond social insects, the testing of evolutionary theories has extended to both ver- tebrates and invertebrates. In long-lived species such as birds and mammals, ageing patterns appear strongly tied to extrinsic mortality risk, with reduced predation pres- sures often associated with increased longevity [13]. In laboratory model organisms, such as *Drosophila melanogaster* and *Caenorhabditis elegans*, experimental manip- ulations have provided direct support for key predictions of these theories. Dietary restriction and mutations in nutrient-sensing pathways, such as insulin/IGF signaling, extend lifespan, providing mechanistic evidence for the trade-offs highlighted in dis- posable soma theory [14]. These models have also demonstrated the molecular basis of antagonistic pleiotropy, where genes that enhance early reproductive success can drive late-life decline.

Taken together, while the classical theories of ageing remain powerful concep- tual frameworks, they fall short when applied to complex cooperative systems like eusocial insects. A more complete evolutionary theory must incorporate social struc- ture, inclusive fitness, and colony-level trade-offs, bridging ecological and mechanistic perspectives.

3 Looking Forward: Towards a New Theory

3.1 Transfers and Selection

In many species, individuals who are no longer reproductively active still contribute significantly to the survival and success of their kin. This contribution takes the form of transfers—care, protection, food provisioning, or other resources—that enhance the survival of offspring and younger group members. Such behavior suggests that natural selection may favor survival beyond reproductive years if post-reproductive individuals continue to generate fitness benefits indirectly.

Studies on primates provide strong evidence for this view. For instance, Lee [4] has argued that transfers, rather than births alone, shape the dynamics of senescence in social species. Individuals who invest heavily in supporting offspring and kin often experience longer survival, indicating that parental and cooperative investment is not simply a byproduct of social living but a driver of evolutionary fitness. In this frame- work, the force of selection on mortality is determined not only by remaining fertility but also by the balance of cumulative transfers—resources received during youth and resources given later in life. Once individuals begin providing transfers, these contri- butions offset earlier dependence, altering the trajectory of the force of selection across age.

3.1.1 The Force of Selection

Hamilton’s pioneering work demonstrated that the force of natural selection declines monotonically with age, making senescence inevitable [3]. He derived age-specific indi- cators quantifying how changes in survival or fertility at a given age affect overall fitness. As summarized by Baudisch [15], these indicators decrease with age because fertility and survival contribute less to reproductive value in later life. From this perspective, ageing emerges as a natural consequence of declining selection pressure.

However, once transfers are incorporated into the framework, the picture becomes more complex. The force of selection can be conceptualized as a weighted average of two effects: the fertility effect, based on remaining reproductive potential, and the transfer effect, based on cumulative net support to others. The fertility effect favors the survival of individuals who can still reproduce, while the transfer effect favors those who contribute resources to their kin. Together, they generate a hump-shaped curve of selection pressures, where survival is optimized not only at reproductive ages but also at ages where transfers provide maximum benefit to kin.

This broader framework highlights that natural selection does not simply maximize fertility. On the ascending left side of the curve, increasing fertility is advantageous for population growth. At the peak, fertility and transfers are in balance, representing the point of maximum selection pressure. Beyond the peak, transfers dominate: survival is maintained because older individuals enhance the fitness of their relatives through care and provisioning. This is especially relevant to humans and highly social animals, where cooperation and resource transfers underpin life histories and social structure.

Table 3 Comparison of fertility-based and transfer-based forces of selection.

Dimension	Fertility-Based Selection	Transfer-Based Selection
Primary Driver	Remaining reproductive potential	Net transfers (resources given vs. received)
Effect on Mortality	Survival is favored until fertility declines	Survival is favored as long as transfers provide fitness benefits
Predicted Outcome	Decline in selection pressure with age, leading to inevitable senescence	Extended survival beyond reproduction if transfers enhance kin fitness
Species Examples	Most solitary species (e.g., short-lived insects)	Humans, primates, eusocial species with cooperative brood care

Overall, natural selection does not act solely on fertility but also on transfers, mak- ing cooperation and support within populations central to the evolution of ageing. The equilibrium point where transfers dominate selection appears to be the evolutionary position of humans and many other highly social species.

4. Population Equilibrium and the Evolutionary Trajectory to the Optimal Equilibrium

Population equilibrium, when framed with intergenerational transfers, provides a powerful way of understanding the joint dynamics of age distribution, fertility, and survival. As described in Lee's model [4], the renewal equation links consumption with fertility and mortality, producing a renewal curve that describes population growth. Equilibrium occurs at the intersection of the consumption curve and the renewal curve, where the growth rate falls to zero and the system stabilizes. In this formulation, intergenerational transfers play a central role, as they mediate the balance between consumption needs and reproductive investment across age groups.

3.2 Trajectories to Optimal Equilibrium

The concept of an optimal equilibrium emerges from the hump-shaped balance curve described in the theory. At this peak, fertility and parental investment are optimally balanced, ensuring that the population maximizes its long-term growth rate. Natu- ral selection and mutation pressures continually guide populations toward this point [15]. The evolutionary trajectory toward the optimal equilibrium can be understood through several key mechanisms.

First, the optimal equilibrium represents the evolutionary attractor of the system, where resource allocation between fertility and survival is stabilized. This is the point where populations achieve maximum efficiency in converting resources into reproduc- tive success, balancing parental investment with the number of offspring. Mutations that align with this balance are positively selected, reinforcing the trajectory toward the equilibrium.

Second, counterintuitive selection processes can arise. For instance, a reduction in mortality at age zero, which is biologically equivalent to increased fertility, does not shift the balance curve but elevates the renewal curve. This may eliminate the original equilibrium and paradoxically result in the positive selection of higher mortality at age zero. Such outcomes underscore the nonlinear interactions between fertility, mortality, and investment, highlighting that selection does not always operate in an intuitive direction.

Third, the effects of mutations on mortality vary with age. A decrease in mortality at younger ages typically leads to strong positive selection, as it enhances both fertility and survival. By contrast, reducing mortality at intermediate ages may produce mixed outcomes, with negative selection pressure near birth but positive pressure at the upper bounds of reproductive age. The result is a crossover pattern that emphasizes the complex interplay of age-specific selection pressures.

Fourth, as population size increases, density dependence becomes more significant. This manifests as a downward shift in the balance curve, reflecting the resource limi- tations imposed by higher density. Such shifts push populations closer to the peak of the hump-shaped curve, effectively stabilizing them at the optimal equilibrium. This adaptation represents a form of evolutionary tuning to population pressure and finite resources [4].

Ultimately, the evolutionary process culminates in populations converging on the optimal equilibrium. Even at this point, mutations that reduce mortality remain advantageous, ensuring a continual refinement of survival and reproductive strategies. The optimal equilibrium is not static but represents a dynamic balance maintained through ongoing mutation and selection processes.

A useful comparative framework is provided by Kaplan and Robson's model of the coevolution of brain size and longevity in primates and humans [16]. Their approach emphasizes intergenerational transfers within a population-level constraint but differs from the transfer-based equilibrium theory in crucial ways. Kaplan and Robson model productivity as a function of human capital rather than fertility, and they do not explicitly incorporate mutation–selection dynamics.

Table 4 Key implications of the balance curve and optimal equilibrium in evolutionary dynamics.

Mechanism	**Implication for Population Dynamics**
Optimal Equilibrium	Peak of the balance curve where fertility and investment are optimally balanced, maximizing population growth.
Counterintuitive Selection	Reductions in early mortality can destabilize equilibria, sometimes favoring unexpected outcomes such as positive selection for mortality at age zero.
Mutation Effects	Age-specific changes in mortality may be positively or negatively selected depending on where they occur, creating crossover points in selection pressure.
Density Dependence	Increasing population size shifts the balance curve downward, driving populations closer to the optimal equilibrium.
Evolutionary Outcome	Populations converge to the optimal equilibrium, where trade-offs between fertility and survival stabilize long-term growth.

As a result, their framework does not inherently predict biological ageing or rising mortality without additional assumptions. While both approaches recognize the centrality of transfers in human evolution, Lee's theory integrates fertility and mortality within a mutation–selection framework, thereby linking demographic patterns directly to the biology of ageing.

4.1 Comparative Ageing Across Taxa

One of the most striking features of ageing is the extraordinary diversity of lifespan and senescence patterns across the tree of life. While classical theories of ageing predict a universal decline in fertility and survival with age [3], empirical evidence demonstrates that species exhibit a wide range of ageing trajectories, including negligible and even negative senescence. Comparative studies across taxa provide essential insights into both the universality and limits of evolutionary ageing theories.

In mammals, lifespans vary from a few years in small rodents to over two centuries in the bowhead whale [17]. The naked mole-rat is a particularly striking outlier: despite being a small rodent, it shows negligible senescence and exceptional resistance to age- related disease [18]. Birds generally live longer than mammals of similar body size, a pattern attributed to lower extrinsic mortality and metabolic adaptations [19].

Among insects, eusocial taxa such as ants, termites, and bees exhibit some of the most dramatic lifespan differences. Queens of many ant species may live for decades, while workers live only months [20]. These differences cannot be explained solely by mutation accumulation or antagonistic pleiotropy, but instead reflect colony-level selection and division of reproductive labor [21]. By contrast, solitary insects typically follow the classical pattern of short lifespans and rapid senescence.

Reptiles and amphibians often show slow or negligible senescence, with some turtles living for over a century and showing little age-related decline in fertility or sur- vival [22]. Similarly, several fish species such as rockfish and Greenland sharks exhibit extreme longevity and negligible senescence, challenging the assumption that ageing is universal [23].

Table 5 Examples of lifespan and senescence patterns across taxa.

Taxa	**Lifespan Range**	**Senescence Pattern / Notes**
Mammals	Mice: ∼3 years; Bowhead whale: > 200 years	Wide variation; naked mole-rat shows negligible senescence.
Birds	Small passerines: 5–10 years; Albatross: 60+ years	Longer lifespans than mammals of similar size; delayed senescence.
Insects	Workers: months; Ant queens: Decades	Extreme caste divergence; longevity linked to reproductive role.
Reptiles / Amphibians	Many turtles: > 100 years	Negligible or slow senescence; longevity linked to low extrinsic mortality.
Fish	Rockfish: > 200 years; Greenland shark: ∼400 years	Some of the longest-lived vertebrates; negligible senescence.
Basal Metazoans	Hydra: indefinite lifespan	Experimentally negligible senescence; stable mortality/fertility with age.

Comparative biology demonstrates that ageing is neither uniform nor inevitable across species. Instead, senescence appears as one of several possible evolutionary trajectories, shaped by ecological pressures, life history trade-offs, and, in the case of social species, group-level dynamics. These findings suggest that universal ageing theories must be supplemented by taxon-specific and ecological considerations.

6 The Evolution of Post-Reproductive Lifespan: Menopause and the Grandmother Hypothesis

Unlike most species, humans and a few long-lived cetaceans (notably killer whales and pilot whales) exhibit a prolonged post-reproductive lifespan, in which indi- viduals survive for decades after ceasing reproduction [25, 26]. This phenomenon challenges classical evolutionary theories of ageing, which predict that selection pres- sure declines to zero once reproduction ends [3]. The persistence of menopause and extended post-reproductive survival has motivated new hypotheses linking longevity to intergenerational transfers and inclusive fitness.

6.1 Menopause as an Evolutionary Puzzle

In most mammals, reproductive capacity continues until death, with no clear menopause. In contrast, human females typically undergo menopause in midlife, with a substantial proportion of their lifespan spent in a non-reproductive state. From a strictly fertility-based perspective, this should reduce direct fitness, and thus the persistence of menopause appears paradoxical.

Early hypotheses framed menopause as a by-product of modern longevity or as a non-adaptive consequence of follicular depletion. However, demographic and anthropological evidence suggests that post- reproductive survival has been maintained by natural selection due to indirect fitness benefits.

6.2 The Grandmother Hypothesis

The “grandmother hypothesis” provides one of the most influential adaptive explana- tions for menopause. According to this hypothesis, post-reproductive females enhance their inclusive fitness not by producing more offspring, but by increasing the survival and reproductive success of their descendants through transfers of food, knowledge, and care [25, 27]. In this framework, menopause reflects a life-history strategy where the indirect fitness benefits of supporting grandchildren outweigh the direct benefits of bearing additional offspring at older ages, which may be costly or risky.

Anthropological studies of hunter-gatherer populations support this idea, showing that grandmothers often make substantial contributions to child survival and mater- nal fertility. These contributions align with Lee’s broader framework on the force of selection through transfers, which emphasizes that natural selection operates not only via fertility but also through resource flows across generations [4].

6.3 Comparative Evidence from Non-Humans

Although menopause is rare in the animal kingdom, evidence for extended post- reproductive lifespan exists in killer whales (*Orcinus orca*) and short-finned pilot whales (*Globicephala macrorhynchus*) [26]. In these species, older females often play leadership roles, guiding pods during food scarcity and increasing the survival of kin. This convergent pattern suggests that menopause and post-reproductive lifespan evolve under conditions where kin-directed benefits of older individuals are strong and where ecological or social structures support prolonged survival.

Table 6 Examples of species with extended post-reproductive lifespan.

Species	**Post-Reproductive Duration**	**Notes / Adaptive Explanation**
Humans (*Homo sapiens*)	Decades (typically 30–40% of lifespan)	Menopause around midlife; support to grandchildren through transfers, care, and knowledge.
Killer whales (*Orcinus orca*)	Up to 40 years post-reproductive	Older females lead pods and increase kin survival during ecological stress.
Pilot whales *macrorhynchus*)	Several decades	Similar pattern to killer whales; kin support and group cohesion.
Other mammals (e.g., elephants, chimpanzees)	Limited evidence of reproductive cessation	Older females contribute to social knowledge transfer, but no clear menopause.

6.4 Implications

The evolution of post-reproductive lifespan highlights the importance of inclusive fit- ness, intergenerational transfers, and social structure in shaping human ageing. It also provides a critical example of how classical fertility-based models must be extended to incorporate kin selection and transfers. The convergence of post-reproductive lifespan in humans and cetaceans suggests that menopause may evolve under specific ecolog- ical and social conditions where older individuals provide unique benefits to kin that outweigh the costs of lost fertility.

7 Challenges and Controversies in Ageing Theory

A persistent challenge for evolutionary theories of ageing is the observation that senes- cence is neither universal nor uniform across the tree of life. Although the classical decline of Hamilton's forces suggests that ageing is an inevitable outcome of weakening selection with age [3], comparative work reveals taxa with negligible senescence, delayed senescence, and even patterns consistent with "negative senescence," in which survival or fecundity increase with age [28, 29]. Hydra display constant mortality over time [24], several turtles and fish species show little age-related deterioration in survival or reproduction, and some social insects combine extreme longevity with high fecundity in queens. These findings do not falsify the logic of declining selection per se, but they expose boundary conditions—ecological, physiological, and social—that can reshape the expression of ageing.

The existence of negligible or negative senescence raises a mechanistic and eco- logical puzzle: why does damage not inevitably accumulate to drive deterioration? In some species, low extrinsic mortality, indeterminate growth, and continuous somatic maintenance appear to buffer late-life decline. In eusocial species, division of labor and colony-level selection alter trade-offs such that fecundity and longevity may be jointly elevated in queens. These cases suggest that the mapping from evolutionary forces to observable senescence is mediated by life-history architecture, resource flows, and repair capacities, rather than being a simple, monotonic consequence of age alone.

A second, enduring controversy concerns the tension between mutation accumula- tion and adaptive (or "programmed") ageing hypotheses. The predominant view holds that ageing is a non-adaptive byproduct of selection favoring early-life fitness (via mutation accumulation and antagonistic pleiotropy), with disposable soma providing a mechanistic bridge to resource allocation and repair deficits [1, 2, 10]. Proponents of adaptive ageing have argued that late-life deterioration might, under specific ecological structures (e.g., density regulation, kin-selected contexts, or group-level benefits), be directly favored by selection. However, mainstream evolutionary biology remains skeptical of direct adaptationist accounts, emphasizing that any appearance of "programming" can emerge from conserved growth and nutrient-sensing pathways whose late-life activity becomes maladaptive ("quasi-programs") [30, 31]. The weight of evidence continues to favor non-adaptive origins modulated by constraint and pleiotropy, while allowing that demographic structure and transfers can substantially modify age patterns of selection. A third frontier is the question of inevitability: can ageing be decelerated or "engineered away"? Interventions that target conserved longevity pathways—such as reduced insulin/IGF signaling, dietary restriction, and pharmacologic mTOR inhibition—extend lifespan and healthspan in multiple model organisms [7, 14, 32]. These results demonstrate that the rate of ageing is plastic and, at least in part, mechanistically tractable. Yet the translation to long-lived species, including humans, confronts deep trade-offs. Reduced growth and fertility, impaired wound healing, immune modulation, and context-dependent frailty highlight the evolutionary entan- glement between pathways that promote early-life fitness and those that drive late-life decline. Moreover, demographic feedbacks and ecological constraints imply that population-level consequences of decelerated ageing (e.g., changed age structures, resource demands) must be weighed alongside individual benefits.

Together, these controversies underscore that ageing emerges from an interaction among evolutionary forces, ecological environments, and molecular programs. The central theoretical task is not to replace Hamiltonian logic, but to embed it within a richer life-history and mechanistic framework that explains when and why senescence is weak, negligible, or apparently reversed. Progress will depend on integrative models that connect selection gradients to repair economics and pathway dynamics, coupled with comparative datasets spanning taxa, ecologies, and social systems.

Table 7 Selected controversies in ageing theory and current points of tension

Controversy	**Evidence and Challenges**	**Key Open Questions**
Negligible / Negative Senes-Cence	Hydra, some turtles and fish, and exceptional insect queens show weak or absent late-life decline [24, 28].	What life-history architectures and repair regimes permit negligible senes-cence despite mutation pressure?
Non-adaptive vs. Adaptive Ageing	Classical view: byproduct of early-life selection (MA/AP/DS) [1, 2, 10]; adaptive accounts remain controversial [30].	Can any robust, general conditions yield direct selection for ageing, or are observed patterns fully explainable by pleiotropy and constraints?
Engineering Ageing	mTOR/IGF targeting, dietary restriction, and other interventions extend lifespan in models [7, 14, 32].	What are the trade-offs for long-lived species? Can healthspan be expanded without unacceptable costs to fertility, immunity, or resilience?

8 Discussion and Conclusion

The evolution of ageing remains one of the most profound questions in biology, cutting across genetics, demography, ecology, and social organization. Classical theories— mutation accumulation, antagonistic pleiotropy, and the disposable soma—provided foundational explanations for why senescence arises despite its detrimental effects late in life. Yet, as this review has highlighted, these frameworks are not sufficient to account for the diversity of ageing patterns observed across taxa. The longevity of eusocial insect queens, the negligible senescence of hydra and some reptiles, and the extended post-reproductive lifespan of humans and certain cetaceans all defy predic- tions derived solely from fertility-based fitness. These cases compel us to recognize the role of kin-directed transfers, ecological structure, and colony-level or group-level benefits in shaping the trajectory of ageing.

A recurring theme is that the force of selection is not exhausted by direct reproduc- tion. Intergenerational transfers of resources, knowledge, and care can sustain selective pressure well into late life, helping to explain the persistence of long post-reproductive survival in humans and whales. Similarly, colony-level dynamics in social insects gen- erate conditions where extreme longevity can coexist with high fecundity in queens, while workers remain short-lived. These examples illustrate how ageing is molded not only by the decline of fertility but also by the broader social and ecological context in which individuals are embedded.

Mechanistic studies reinforce this pluralistic picture. Nutrient-sensing and repair pathways, once thought to decline passively with age, are now recognized as deeply entwined with life-history trade-offs. Experimental manipulations in model organisms demonstrate the plasticity of ageing, showing that lifespan can be extended through interventions such as dietary restriction, altered insulin/IGF signaling, and mTOR inhibition. Yet these results also underscore the constraints of evolution: pathways that promote early-life growth and reproduction often impose costs in late life, and interventions that delay ageing can carry trade-offs in fertility, immunity, or resilience. The feasibility of "engineering" ageing away therefore remains an open question.

At the same time, comparative and theoretical research exposes challenges that are unresolved. Why do some species show negligible or even negative senescence? Under what ecological and demographic conditions might ageing itself be adaptive, rather than a non-adaptive byproduct of selection? Can inclusive fitness through transfers be formally integrated with molecular and physiological models to provide predic- tive, testable frameworks? These gaps highlight the need for integrative approaches that connect demographic selection gradients, mechanistic pathways, and ecological context.

In conclusion, ageing is not a uniform or inevitable fate dictated by biology alone, but rather the emergent outcome of evolutionary trade-offs, ecological constraints, and social organization. Progress in the field requires bridging classical evolutionary theory with insights from comparative biology, mechanistic studies, and demographic models of intergenerational transfers. Such a synthesis has the potential not only to resolve long-standing paradoxes in ageing theory but also to inform translational efforts aimed at extending human healthspan. By situating ageing at the nexus of evolution, ecology, and physiology, we move closer to understanding both its inevitability and its malleability—and to discerning the conditions under which the burden of senescence can be reduced.

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References

[1]. Medawar, P.B.: An Unsolved Problem of Biology. H.K. Lewis, ??? (1952)

[2]. Williams, G.C.: Pleiotropy, natural selection, and the evolution of senescence. Evolution **11**(4), 398–411 (1957)

[3]. Hamilton, W.D.: The moulding of senescence by natural selection. Journal of Theoretical Biology **12**(1), 12–45 (1966)

[4]. Lee, R.D.: Rethinking the evolutionary theory of aging: transfers, not births, shape senescence in social species. Proceedings of the National Academy of Sciences **100**(16), 9637–9642 (2003)

[5]. Keller, L., Genoud, M.: Queen longevity in social insects. Insectes Sociaux **44**(2), 131–150 (1997)

[6]. Jemielity, S., al.: Short-lived queens outlive their workers. Current Biology **15**(18), 744–745 (2005)

[7]. Harrison, D.E., al.: Rapamycin fed late in life extends lifespan in genetically heterogeneous mice. Nature **460**(7253), 392–395 (2009)

[8]. Mannick, J.B., al.: mtor inhibition improves immune function in the elderly. Science Translational Medicine **6**(268), 268–179 (2014)

[9]. Charlesworth, B.: Evolution in Age-Structured Populations. Cambridge Univer- sity Press, ??? (1994)

[10]. Kirkwood, T.B.L.: Evolution of ageing. Nature **270**(5635), 301–304 (1977)

[11]. Keller, L., Jemielity, S.: Extraordinary lifespans in ants: a test of evolutionary theories of ageing. Nature **389**(6654), 958–960 (1997)

[12]. Kramer, B.H., Schaible, R.: Lifespan evolution in eusocial workers—a theoretical approach to the effects of extrinsic mortality in a hierarchical system. PLoS One **11**(3), 0150060 (2016)

[13]. Partridge, L., Barton, N.H.: The evolutionary biology of ageing: insights from drosophila. Nature Reviews Genetics **2**(11), 870–880 (2001)

[14]. Kapahi, P., Kaeberlein, M., Hansen, M.: Dietary restriction and lifespan: Lessons from invertebrate models. Ageing Research Reviews **39**, 3–14 (2017)

[15]. Baudisch, A.: Hamilton's indicators of the force of selection. Proceedings of the National Academy of Sciences **102**(23), 8263–8268 (2005)

[16]. Kaplan, H., Robson, A.J.: The coevolution of human longevity and intelligence with intergenerational transfers. Proceedings of the National Academy of Sciences **99**(15), 10221–10226 (2002)

[17]. George, J.C., Bada, J., Zeh, J., Scott, L., Brown, S., O'Hara, T., Suydam, R.: Age and growth estimates of bowhead whales (balaena mysticetus) via aspartic acid racemization. Canadian Journal of Zoology **77**(4), 571–580 (1999)

[18]. Buffenstein, R.: Negligible senescence in the longest living rodent, the naked mole- rat: insights from a successfully aging species. Journal of Comparative Physiology B **178**(4), 439–445 (2008)

[19]. Holmes, D.J., Austad, S.N.: Comparative biology of aging in birds: an update. Experimental Gerontology **36**(4-6), 869–883 (2001)

[20]. Keller, L., Genoud, M.: Eusociality: controlling the costs of altruism and cooperation. Trends in Ecology & Evolution **12**(3), 99–103 (1997)

[21]. Kramer, B.H., Schaible, R.: The evolution of longevity in eusocial insects. Annual Review of Entomology **61**, 1–20 (2016)

[22]. Congdon, J.D., Nagle, R.E., Kinney, O.M., Loben Sels, R.C.: Senescence and reproductive output in the long-lived turtle chrysemys picta. Ecology **82**(3), 788– 798 (2001)

[23]. Nielsen, J., Hedeholm, R.B., Heinemeier, J., Bushnell, P.G., Christiansen, J.S., Olsen, J., Ramsey, C.B., Brill, R.W., Simon, M., Steffensen, J.F., *et al.*: Eye lens radiocarbon reveals centuries of longevity in the greenland shark (somniosus microcephalus). Science **353**(6300), 702–704 (2016)

[24]. Mart´ınez, D.E.: Mortality patterns suggest lack of senescence in hydra. Experi- mental Gerontology **33**(3), 217–225 (1998)

[25]. Hawkes, K., O'Connell, J.F., Blurton Jones, N.G.: Grandmothering, menopause, and the evolution of human life histories. Proceedings of the National Academy of Sciences **95**(3), 1336–1339 (1998)

[26]. Foster, E.A., Franks, D.W., Mazzi, S., Darden, S.K., Balcomb, K.C., Ford, J.K.B., Croft, D.P.: Adaptive prolongation of postreproductive lifespan in killer whales. Science **337**(6100), 1313–1313 (2012)

[27]. Lehmann, L., Alger, I., Weibull, J.W.: Menopause: adapting a costly trait. Journal of Theoretical Biology **337**, 47–60 (2013)

[28]. Jones, O.R., Scheuerlein, A., Salguero-G ômez, R., *et al.*: Diversity of ageing across the tree of life. Nature **505**(7482), 169–173 (2014)

[29]. Vaupel, J.W., Baudisch, A., Dölling, M., Roach, D.A., Gampe, J.: The case for negative senescence. Theoretical Population Biology **65**(4), 339–351 (2004)

[30]. Kirkwood, T.B.L., Austad, S.N.: Why we age and why we don't. Nature **408**(6809), 233–238 (2000)

[31]. Blagosklonny, M.V.: Aging as a mtor-driven hyperfunction: a theory of aging. Cell Cycle **11**(7), 1340–1349 (2012)

[32]. L ôpez-Ot´ın, C., Blasco, M.A., Partridge, L., Serrano, M., Kroemer, G.: The hallmarks of aging. Cell **153**(6), 1194–1217 (2013)

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