

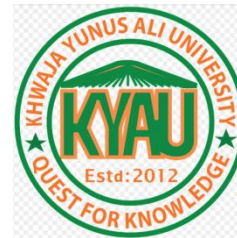
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Research Article

Unveiling the Secrets of Termite Longevity: A Recent Review

Zinat Tamannaa*, Md. Anayet Kabir, Shahidur Rahman, Nushrat Jahan Bushra, Rubait Hasan

Department of Biochemistry and Biotechnology, Khwaja Yunus Ali University, Enayetpur, Chauhali, Sirajganj, Bangladesh.

*Correspondence: zinattamanna.ru@gmail.com (Dr. Zinat Tamannaa, Assistant Professor, Department of Biochemistry and Biotechnology, School of Biomedical Science, Khwaja Yunus Ali University, Sirajganj, Bangladesh)

ABSTRACT

Termites are eusocial insects having different lifespans within a single colony. Within the same colony, the lifespans of social hymenoptera can vary by more than a hundred times. The queens of some social insects, including termites, ants, and certain bees, can survive for several years to decades. In contrast, non-reproductive workers and soldiers have much shorter lifespans, making the queen's longevity a key area of study for understanding the trade-off between reproductive and non-reproductive casts. Because of their extraordinary lifespan, termites are becoming a promising model for aging research. Aging is characterized by a deterioration in homeostatic regulation throughout time, leading to functional decline and an elevated risk of illnesses and mortality. The secrets to the extended lifespan of termite royalty lie in a complex interplay of factors. Various elements contribute to their longevity, from their unique biology and genetic makeup to their diet and environment. This article delves into the scientific revelations about king and queen termites, exploring their antioxidant systems, the role of insulin signaling, and the impact of social immunity on their lifespan. These factors work together to allow the queen to live for decades, ensuring the colony's continued survival and growth. Research into termite aging and longevity continues to shed light on the genetic and molecular mechanisms that underlie their remarkable life spans, offering insights that may have broader implications for aging in other organisms, including humans. In summary, the present study might clarify the mechanisms underlying termite lifespan, which would significantly enhance anti-aging research.

Keywords: Aging, Anti-Aging, Longevity, Queen, Termite.

Introduction

In the fascinating world of insects, king and queen termites stand out for their extraordinary longevity. These royal couples, the cornerstone of termite colonies, can live up to 50 times longer than their worker counterparts. The royal couples, forming the cornerstone of termite colonies, exhibit an extraordinary ability to defy aging, living for decades while maintaining nearly maximal fertility. This remarkable

KYAU Journal, 7(1): 19-26

lifespan has piqued the interest of scientists, leading to groundbreaking research on aging and longevity in social insects. The lifespan disparity between termite royalty and other insects is truly astounding. While most solitary insects have relatively short lives, king and queen termites can live for decades (Tasaki *et al.*, 2023). Queens of several termite species can survive for over 20 years while sustaining nearly maximal fertility (Tasaki *et al.*, 2021). In stark contrast, the median lifespan of sterile workers in the same species is a mere 56 days (Séité *et al.*, 2022). A study on *Cryptotermes secundus* queens achieves remarkable longevity, living up to 13 years compared to shorter-lived insects like *Drosophila melanogaster* (Kuhn *et al.*, 2020). Key findings reveal that aging in these queens is non-linear, with significant gene networks related to stress response and proteostasis becoming active later in life.

The biology of king and queen termites is a fascinating subject that showcases remarkable adaptations for their roles as colony founders and primary reproducers. These royal pairs exhibit unique physical and reproductive characteristics that set them apart from other termite castes. King and queen termites undergo significant physical changes after establishing a colony. The reproductive system of termite queens is highly efficient, with specialized organs and physiological processes that support continuous egg production. The first five months after colony foundation are critical for the survival and establishment of a new termite colony. During this period, the founding king and queen had limited internal resources and successfully established their first brood (Chouvenc *et al.*, 2023). If they succeed, both parents display extensive biparental care to their offspring, resulting in the emergence of about a dozen larvae. As the colony grows, parental care duties gradually shift from the king and queen to the workers. This transition marks the establishment of the reproductive division of labor, with the royal pair focusing solely on reproductive output (Chouvenc *et al.*, 2023). The colony then enters a phase of exponential growth, which eventually slows down as the queen reaches her maximum oviposition capacity. The nutritional requirements of termites vary depending on caste and developmental stage. Workers mostly need carbohydrates to maintain energy expenditure, while larvae need protein to promote their growth (Poissonnier *et al.*, 2020). In higher termite species like *Nasutitermes exitiosus*, only major workers forage, while larvae, soldiers, and minor workers receive regurgitated food from the major workers through trophallaxis. Interestingly, termites display a preference for foods with higher nitrogen content, such as wood with fungal decomposition, lichens, and lower parts of the litter (Poissonnier *et al.*, 2020). Secondary plant compounds, carbohydrate content, and digestibility also play a role in food selection by termites. However, the capacity of termites to protect an intake target and the significance of the macronutrient ratio in meal choices are still unclear.

Interestingly, some termite species have developed unique reproductive strategies. The exceptional reproductive capacity of termite royalty is sustained by a range of specialized physiological adaptations. For example, queens of *Reticulitermes speratus* have considerably higher antioxidant enzyme activity than non-reproductive termites (Tasaki *et al.*, 2021). This enhanced antioxidant system helps protect the queen from oxidative damage, contributing to her longevity and sustained fertility. King and queen termites possess remarkable biological adaptations that enhance both their physical traits and reproductive capabilities. These features allow them to maintain high fertility over exceptionally long lifespans, making them unique subjects for studies on aging and reproduction in insects. A review of termite reproduction has been examined previously (Tasaki *et al.*, 2021), but there is no recent review to comprehend the updated facts regarding their lifetime. In this review, we tried to reveal the science behind the mystery of termite longevity that will impact a state-of-the-art in the field of anti-aging research.

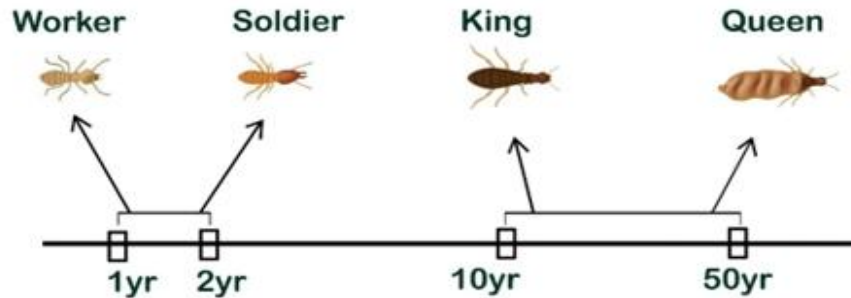


Figure 1: Life span of termite casts

Brain Plasticity and Division of Labor

Sociality is linked to greater longevity and increased plasticity in aging rates, as seen in reproductive termites and ants, which live much longer than their non-reproductive nest mates. The authors call for reliable transcriptomic markers and a comprehensive theory of aging in social animals, factoring in the reproductive roles of workers and the late maturity of queens (Korb & Heinze *et al.*, 2021). Termite brain morphology varies based on caste, age, and role within the colony. Reproductive termites have larger brains, with alates having particularly large optic lobes due to their reliance on vision outside the nest, unlike ergatoids and nymphoids who stay inside. Brain size decreases with age, especially in primary kings, whose optic lobes shrink significantly, leading to reduced visual function. Overall, the study highlights the adaptive changes in brain morphology in termites, driven by both caste-specific roles and age, suggesting that brain plasticity plays a crucial role in the evolution of social organization in these insects (Ishibashi *et al.*, 2023).

Molecular regulation of lifespan extension

A study investigates how sociality in insects has contributed to the divergence in lifespan between reproductive and sterile castes. It identifies important longevity genes and mechanisms involved in insect social development and emphasizes the long-term implications of fertility induction (Negroni *et al.*, 2021). In the ant *Temnothorax rugatulus*, workers made fertile in the absence of a queen live longer and show up-regulation of genes related to longevity and reproduction. Even after returning to their queen, workers retain high expression of these genes, despite intermediate ovary development. By contrasting foragers and builders in *Macrotermes bellicosus*, this study examined the molecular mechanisms underlying job division in termite workers. The result confirmed the hypothesis that foragers have worse physiological circumstances, builders have gene expression profiles more similar to queens, and builders invest more in anti-aging mechanisms (Elsner *et al.*, 2021).

Telomerase activity

In termite species like *Prorhinotermes simplex*, the activation of telomerase, an enzyme that lengthens telomeres, is notably higher in the somatic tissues of kings and queens than in those of sterile castes. This contrasts with many other animals, where telomerase is downregulated in somatic tissues to prevent uncontrolled growth (Koubová *et al.*, 2021). Despite this increased telomerase activity, the researchers did not observe differences in telomere lengths between castes, suggesting that telomere length may not be the primary factor behind the longevity of termite reproduction. The findings align with the broader hypothesis that telomerase is associated with longevity, but the exact mechanisms by which it influences lifespan in termites remain unclear (Koubová *et al.*, 2021). The differences in transposable elements (TEs) regulation between sterile and non-sterile castes in the termite *Macrotermes natalensis*. TEs are mobile genetic

KYAU Journal, 7(1): 19-26

elements that can cause genomic damage over time. In termites, TEs are better regulated in queens compared to workers, likely due to the queens' reproductive longevity. The study found that TE regulation via the piRNA pathway, which regulates TEs, is significantly upregulated in queens, particularly in older queens. To prevent TE-induced genomic instability. This regulation was less effective for workers. Workers exhibit higher TE expression compared to queens. However, queens show efficient suppression of TEs, especially as they age, likely contributing to their extended lifespans. Reduced TE activity in queens may protect their genome integrity and support their extreme longevity and continuous reproductive output. The research provides insights into how termites' reproductive castes manage genomic integrity over long lifespans through effective TE regulation (Post *et al.*, 2023). The expression of telomerase in somatic tissues suggests that telomerase may be involved in broader cellular maintenance, stress responses, or metabolic regulation, especially in organisms with distinct life histories like termites (Pangrácová *et al.*, 2024).

Antioxidant Systems in Termite Royalty

The remarkable longevity of king and queen termites has a significant connection to their advanced antioxidant systems. These systems play a crucial role in protecting the royal pair from oxidative stress, which is a major contributor to aging in most organisms. Several factors contribute to the exceptional longevity of king and queen termites. The minimal extrinsic mortality after colonization is a significant factor (Tasaki *et al.*, 2021). Protected within the confines of their royal chamber, they face minimal threats from predators or environmental hazards. The royal diet plays a crucial role in sustaining their long lives. Components of the food provided to kings and queens, such as sphingomyelin and acetyl-l-carnitine, are associated with anti-aging and longevity (Tasaki *et al.*, 2023). This specialized nutrition supports their extended lifespan and reproductive capabilities. Recently, ultra-performance liquid chromatography-tandem mass spectrometry analysis revealed that *Hodotermopsis sjostedti* species contain a significant amount of NMN, a potential anti-aging compound that may also be involved in the longevity of termites (Tamanna *et al.*, 2024). Genetic factors also play a significant part in termite royalty longevity. Research has revealed that kings and queens upregulate genes involved in different lifespan-prolonging mechanisms. These genetic changes support robust mitochondrial functioning and increase genome stability. Termite longevity seems to be uniquely influenced by the insulin signaling system. The insulin-like peptide gene *Iip9* is surprisingly 800-fold upregulated in adult queens and kings (Séité *et al.*, 2022). This apparent insulin increase is associated with sustained fertility without the typical costs of reproduction. The remarkable lifespan of king and queen termites results from a complex interplay of factors, including their protected environment, specialized diet, genetic adaptations, and unique metabolic processes.

Genetic Factors in Termite Longevity

Studies have shown significant variations in gene expression patterns between reproductive and sterile castes in termites. Several key genes and pathways have been identified as crucial players in termite longevity. Research on the subterranean termite *Reticulitermes chinensis* revealed 35 IIS-pathway-associated genes that may contribute to the extended lifespan of reproductive castes (Haroon *et al.*, 2022). Among these genes, phosphoinositide-dependent kinase-1 (Pdk1), protein kinase B2 (akt2-a), mammalian target of rapamycin (mTOR), eukaryotic translation initiation factor 4E (EIF4E), and ribosomal protein S6 (RPS6) have shown significant differences in expression between reproductive and non-reproductive castes. These genes have been associated with various physiological effects, including cell survival, protein synthesis, and metabolism, all of which may contribute to the longevity of kings and queens (Haroon *et al.*, 2022).

Older queens show increased protein synthesis and degradation, a departure from typical aging patterns, and exhibit changes in DNA repair genes like BRCA1, which help maintain genome stability. The research emphasizes the unique aging mechanisms in termite queens that contribute to their long lifespans (Kuhn *et al.*, 2020). The important role of downstream factors like juvenile hormone signaling, vitellogenins, and immune genes in aging and caste-specific physiology, with less focus on the upstream IIS/TOR components. The researchers introduce the TI–J–LiFe network as a novel framework for exploring aging and fecundity in social insects. (Korb *et al.*, 2021). Overall, the genetic factors underlying the extraordinary longevity of king and queen termites involve complex interactions between gene expression patterns, key longevity genes, and defense mechanisms against genomic instability. These findings not only enhance our understanding of aging in social insects but also provide valuable insights into the broader field of aging research (Lin *et al.*, 2021).

The Role of Insulin Signaling Pathway

In termites, as in other organisms, the insulin signaling pathway (IIS-pathway) has a significant impact on physiological aspects of reproduction and lifespan regulation. A study investigated the molecular mechanisms behind the long lifespan of kings and queens in *Macrotermes natalensis* using transcriptomics, lipidomics, and metabolomics. The finding revealed that reproductives share gene expression changes with workers, including upregulation of DNA damage repair and mitochondrial functions, while antioxidant gene expression was downregulated. Surprisingly, reproductive individuals also exhibited upregulation of components of the insulin/insulin-like signaling (IIS) pathway, including Iip9, without leading to harmful fat storage. The queens allocate resources toward oogenesis and maintain low oxidative damage. The findings suggest that addressing all aging-related processes simultaneously is key to preventing aging in these termites (Séité *et al.*, 2022).

Transcriptome analyses revealed reduced expression of the insulin signaling (IIS) pathway in fat bodies, associated with lifespan extension, while reproductive genes were largely unaffected. These results imply that IIS in termites is independent of fecundity pathways, which helps to modify the usual trade-off between longevity and reproduction. According to the study, a protein-enriched diet had no detrimental effects on the survival of *Cryptotermes secundus* termites and did not increase fecundity at the colony or individual level. In fact, queens on a protein-rich diet showed signs of reduced insulin signaling (IIS), which is typically linked to increased lifespan (Rau *et al.*, 2023). De novo transcriptome assembly and analysis of longevity genes reveal the role of the insulin signaling (IIS) pathway in termite *Reticulitermes chinensis* castes, identifying 35 IIS-related genes through transcriptome analysis. Some key genes like Pdk1, akt2-a, and mTOR are involved in processes like cell growth and metabolism, potentially contributing to the extended lifespan of reproductive castes. The research offers insights into termite longevity and suggests further investigation into aging across castes (Haroon *et al.*, 2022).

Environmental Factors Affecting Longevity

Several environmental conditions impact the longevity of king and queen termites within the colony. These conditions play a crucial role in shaping the lifespan and overall health of the royal pair, as well as the workers that support them. Interestingly, research has shown that constant temperatures may impose more stress on termites than variable temperatures. According to a study on *Cryptotermes secundus*, under consistent conditions, the fecundity of the queens and workers as well as their survival were somewhat reduced (Rau *et al.*, 2021). When subjected to consistent temperatures, the transcriptome profiles of both castes displayed indications of aging. Surprisingly, under constant conditions, workers showed a greater oxidative stress defense signal than queens (Rau *et al.*, 2021). This research emphasizes that environmental

stress, specifically constant temperature exposure, accelerates aging and oxidative stress, with caste and reproductive potential influencing how termites cope with these stresses (Rau *et al.*, 2021).

The diet and nutrition of termite royalty play a crucial role in their longevity. In many organisms, increasing reproductive effort correlates with a shorter lifespan. Social insect queens, such as termite queens, seem to defy this trade-off, too, as they are incredibly fecund and long-lived (Rau *et al.*, 2023). Interesting findings have come from studies on how a diet high in protein affects termites' life-history characteristics. Contrary to expectations based on studies of solitary insects, protein enrichment did not lead to reduced lifespan and increased fecundity at the colony level in termites. Rather, fecundity appeared to be unaltered, but mortality was decreased on an individual basis in queens and workers who ate more of the protein-enriched diet (Rau *et al.*, 2023). A study investigates the effects of food availability on fecundity and lifespan in a social insect, considering both individual and colony dynamics. It found that while survival remained unaffected, queen fecundity decreased, and colony fecundity increased due to workers abandoning cooperation to become sexual. The results demonstrate that even in animals with modest levels of sociality, cooperation, and social behaviors can influence life-history trade-offs (Lin *et al.*, 2023). Understanding these aspects can help us better understand how social insects age and have extended lives.

Future perspectives

The study of termite royalty has revealed several mechanisms that could potentially be applied to human aging research. A key finding highlights the significance of targeting multiple aging processes concurrently, such as the insulin/insulin-like growth factor (IGF-1) signaling and the target of rapamycin (mTOR) pathways. These mechanisms are essential for overcoming the fecundity/longevity trade-off in termites and hold broad implications for human aging. In organisms from fruit flies to humans, dysregulation of these nutrient-sensing pathways leads to disrupted lipid metabolism and the onset of age-related conditions such as type 2 diabetes and insulin resistance (Séité *et al.*, 2022). The study of telomerase activity in termite reproduction also has potential implications for human aging research. While the direct phenotypic impact of telomerase activation in termites remains to be fully elucidated, the association between telomerase and longevity observed in these insects aligns with findings in vertebrates (Koubová *et al.*, 2021). This suggests that further investigation into telomerase-mediated mechanisms could yield valuable insights applicable to human aging.

According to recent studies, termite queens exhibit a non-linear senescence pattern, with an abrupt physiological upheaval occurring as they age (Monroy Kuhn *et al.*, 2021). This finding highlights the importance of conducting time-series analyses that cover the entire lifetime of these long-lived individuals to fully understand the aging process. Investigating how colony-level defenses contribute to the extended lifespan of reproductive could provide insights into the connection between immune function and aging in social contexts (Séité *et al.*, 2022). Today, omic technologies reveal the complexity of termite gut ecosystems, including bacteria, archaea, and protists that help termites digest wood. The synergistic relationship between termites and microbes calls for integrating classical and modern techniques in future research, focusing on microbial impacts on termite physiology and symbiosis evolution (Scharf *et al.*, 2021). By unraveling the mechanisms that allow these insects to achieve exceptional longevity while maintaining high reproductive output, researchers may uncover new strategies for promoting healthy aging in humans and other species.

Conclusion

The unique longevity and high fertility of king and queen termites' contrast with most insects that experience reduced lifespans with reproduction. This phenomenon provides important insights into aging,

KYAU Journal, 7(1): 19-26

highlighting several key factors that contribute to extending lifespans in social insects. The research on termite longevity, including mechanisms like antioxidant systems and insulin signaling, holds the potential to inspire breakthroughs in human aging. These findings suggest unique therapeutic options for encouraging healthy aging and increasing human longevity in future research.

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Authors Contributions

Zinat Tamanna conceptualized the research and supervised the study. The research design was developed by Zinat Tamanna and Md. Anayet Kabir, while Md. Anayet Kabir also contributed to figure interpretation. Software system support was provided by Shahidur Rahman and Rubait Hasan. The literature search was conducted by Md. Anayet Kabir and Nushrat Jahan Bushra. Zinat Tamanna and Md. Anayet Kabir were responsible for drafting the manuscript, with critical review contributions from Zinat Tamanna and Rubait Hasan. Article editing was carried out by Zinat Tamanna. All authors reviewed and approved the final version of the manuscript.

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