Eurasia Specialized Veterinary Publication

Entomological Research Letters

ISSN: 3108-639X

2021, Volume 1, Issue 1, Page No: 58-67
Copyright CC BY-NC-SA 4.0
Available online at: www.esvpub.com/

Adult Longevity Cannot Be Interpreted Without Reproductive Timing, Maintenance Costs, and Changing Ecological Opportunity

Kenji Tanaka[1]*, Yui Kobayashi[1], Takeshi Nakamura[2]

[1]Department of Insect Aging and Reproductive Senescence, Graduate School of Life Sciences, University of Tokyo, Tokyo, Japan.
[2]Department of Ecological Demography and Life Span, Graduate School of Agriculture, Kyoto University, Kyoto, Japan.

***E-mail** ✉ tanaka.kenji@mail.ecc.u-tokyo.ac.jp

ABSTRACT

Adult longevity is commonly treated as a compact indicator of life-history performance, yet equal numbers of adult days can represent very different biological states. An insect may survive while reproductive output has already declined, while costly maintenance processes are sustaining function, or while ecological conditions have sharply reduced the opportunity to convert survival into future reproduction. This conceptual analysis argues that chronological lifespan should therefore be interpreted jointly with reproductive timing, somatic maintenance and repair, and the ecological opportunity structure in which mortality is realized. Evidence from *Drosophila*, wild crickets, beetles, butterflies, bees, ants, and termites shows that these dimensions can dissociate: reproductive effort does not invariably shorten life, dietary effects depend on limiting resources, functional decline can vary independently of age, and fertility can coincide with enhanced stress resistance in some eusocial states. The analysis develops a proposed decomposition of adult longevity that separates chronological persistence from functional persistence, reproductive schedule, maintenance state, and residual ecological opportunity. The framework is intentionally non-quantitative: it does not assign universal weights or infer fitness from lifespan alone. Instead, it identifies when longevity comparisons are biologically informative, when they are ambiguous, and which measurements are required to distinguish alternative explanations. The resulting interpretation is bounded by taxon, sex, social organization, environmental setting, and laboratory-to-field transfer.

Keywords: Adult lifespan, Reproductive timing, Somatic maintenance, Senescence, Residual reproductive value, Insect life history

Received: 05 April 2021
Revised: 13 May 2021
Accepted: 17 May 2021

How to Cite This Article: Tanaka K, Kobayashi Y, Nakamura T. Adult Longevity Cannot Be Interpreted Without Reproductive Timing, Maintenance Costs, and Changing Ecological Opportunity. Entomol Res Lett. 2021;1(1):58-67.
https://doi.org/10.51847/1N4GEB4g2U

Introduction

Adult longevity is central to insect life histories, but its interpretation is often compressed into a single question: how long did the adult survive? That question is necessary but not sufficient. Lifespan is one component of an age-structured life history whose biological consequences depend on when reproduction occurs, which functions are retained with age, and how environmental circumstances alter the value of surviving another day [1]. A long-lived adult may maintain high reproductive capacity, persist after reproduction has largely ceased, or survive under conditions in which future mating, oviposition, dispersal, or resource acquisition is improbable. Treating these

© 2021 Entomological Research Letters

states as equivalent risks converting a temporal measurement into an unsupported statement about performance or fitness.

The problem becomes sharper outside standardized laboratory conditions. Senescence in wild insects is expressed under predation, weather, disease, social interaction, and fluctuating resource availability, so observed survival combines intrinsic age-related change with a changing mortality environment [2]. Longitudinal work in a natural population of *Gryllus campestris* showed that actuarial and phenotypic senescence varied substantially among years, demonstrating that one survival curve cannot be assumed to represent a fixed species-level ageing phenotype [3]. Longevity therefore requires ecological as well as chronological interpretation.

The conventional expectation that reproduction necessarily shortens life is also too rigid. Eusocial insects provide strong counterexamples in which fecundity and longevity can be positively associated or experimentally uncoupled [4, 5]. Such systems do not invalidate allocation theory; they show that reproductive state, caste physiology, resource access, and social organization can alter how costs are expressed. Likewise, late-life reproduction in *Tenebrio molitor* can change independently of adult survival, indicating that reproductive senescence and actuarial senescence need not progress in parallel [6].

This article develops a proposed context-adjusted interpretation of adult longevity. The central claim is not that lifespan lacks value, but that chronological persistence becomes biologically interpretable only when placed beside reproductive timing, functional persistence, maintenance and repair demands, and changing ecological opportunity. These dimensions are kept analytically separate because the available evidence does not support a universal conversion among them.

Materials and Methods

Conceptual decomposition of longevity

This non-empirical analysis used a structured conceptual decomposition rather than a statistical synthesis. The evidence base was restricted to recent peer-reviewed insect studies and syntheses capable of supporting specific premises about lifespan, reproduction, maintenance, functional ageing, or ecological context. Evidence was interpreted at the level at which it was measured: transcriptomic associations were not treated as organismal causal mechanisms, laboratory manipulations were not assumed to predict field outcomes, and social-insect caste patterns were not generalized automatically to solitary insects.

The first analytical step was to separate measurements that are often collapsed under "longevity." Multitrait work in *Drosophila* shows why this separation matters: changes in gene expression, reproduction, and lifespan under fluctuating diets do not map one-to-one, so candidate mediators of lifespan cannot be inferred safely from a single outcome [7]. Nutritional evidence likewise indicates that amino-acid effects on lifespan and reproduction depend on dietary composition and nutrient-sensing context rather than a uniform energetic rule [8]. The decomposition therefore treats chronological survival as an endpoint, not as a proxy for all processes that may accompany it.

The second step was to distinguish life-history history from current adult state. Experimental evolution in *Drosophila* found that postponed reproduction repeatedly evolved with longer lifespan, while larval diet produced partly distinct genomic responses [9]. This supports separating reproductive timing and developmental environment from the duration subsequently observed in adults. The resulting conceptual procedure asks four sequential questions: how long did the adult persist; what biologically relevant functions persisted across that interval; when was reproduction realized relative to death; and under what maintenance and ecological conditions did additional survival occur? These questions define an interpretive architecture rather than a validated score. No numerical weights are assigned because the evidence does not establish exchange rates among these dimensions.

Results and Discussion

Chronological lifespan records elapsed survival. Functional lifespan, as used here, refers more narrowly to the interval during which a defined biologically relevant capacity remains sufficiently expressed to matter for the question being asked. The capacity could be locomotor performance, stress resistance, reproductive competence, sensory function, flight capacity, or another system-appropriate endpoint. It should not be assumed from survival alone.

Drosophila experiments illustrate the distinction. Genetic manipulation of methionine metabolism extended survival while also improving several health-related phenotypes, and altered NELF-A activity affected lifespan

together with locomotor, stress-protection, and cellular-maintenance measures [10, 11]. These studies show that survival and function can be measured concurrently; they do not establish that every day gained in lifespan carries the same functional value or ecological consequence. A chronological extension is therefore most informative when the accompanying functional domain is specified.

Age also does not map uniformly onto physiological performance. Genetic analyses of stress responses in *Drosophila* found age-related decline that varied among genotypes, with evidence consistent with both antagonistic pleiotropy and mutation accumulation [12]. Thus, insects of the same chronological age can occupy different functional states. In the field, the problem is compounded by temporal environmental variation: the decade-long *Gryllus* dataset showed that phenotypic and actuarial senescence changed among generations [3]. A lifespan estimate can therefore be accurate as a measure of time while remaining incomplete as a measure of retained function.

This distinction is especially important for comparative studies. Longer adult survival can reflect slower functional deterioration, delayed failure in one specific system, prolonged survival after reproductive or behavioral decline, or simply lower exposure to external mortality. These possibilities are not interchangeable. Functional lifespan should consequently be defined by the biological capacity relevant to the hypothesis, rather than treated as a generic synonym for longevity.

Reproductive timing and residual reproductive value

A lifespan has different life-history meaning depending on where reproduction lies within it. The strongest challenge to a fixed reproduction-longevity trade-off comes from studies that measure reproductive effort over known adult histories. In wild *G. campestris*, individuals with high early reproductive effort did not show the predicted reduction in later survival [13]. Because this is observational field evidence, condition and ecological opportunity remain possible contributors, but the result is sufficient to reject the assumption that high early effort must always reveal itself as shorter life.

Manipulating the social conditions around mating can also redistribute reproduction across age. In *Drosophila*, male mating history shifted female reproduction toward earlier life and shortened female lifespan, yet this schedule change did not translate straightforwardly into a different intrinsic population-growth proxy [14]. Timing therefore carries information that lifetime totals can hide. Two females with similar cumulative reproduction can expose offspring production to different environmental windows and can retain very different amounts of future reproductive opportunity at the same chronological age.

Resource identity further complicates apparent allocation costs. In female *Drosophila*, dietary cholesterol availability changed the lifespan response to protein, showing that a limiting sterol can mediate an apparent reproduction-longevity trade-off [15]. Dietary restriction experiments under injury and infection likewise showed that lifespan responses depend on nutritional and challenge context rather than a single axis of "more maintenance versus more reproduction" [16]. These findings argue against treating somatic cost as a universal energetic debit.

The same principle extends to activity. In *Melitaea cinxia*, flight and food availability altered reproduction and lifespan in treatment-dependent ways [17]. Survival gained under abundant resources is not equivalent to survival achieved while flight, feeding, or reproductive opportunity is constrained. In *Bombus terrestris* colonies, the value of continued queen survival also changes with expected future fecundity and the workers' opportunity to inherit reproduction [18]. That social-insect result should not be converted into a universal numerical estimate of residual reproductive value, but it demonstrates the more general point: the biological value of remaining alive depends partly on what reproduction is still possible.

Accordingly, residual reproductive value is used here as a qualitative interpretive variable rather than a calculated quantity. Additional adult days should be interpreted differently when they occur before peak reproduction, during sustained reproduction, after marked reproductive decline, or in an environment where reproduction is unlikely to be realized. Chronological lifespan alone cannot distinguish these states.

Somatic maintenance and repair costs

Longevity also depends on what must be maintained to preserve survival and function. "Somatic maintenance" is often invoked as though it were a single resource pool, but the insect evidence is more heterogeneous. In *Drosophila*, reducing germline proliferation altered immune-gene expression after infection, supporting an interaction between reproductive state and immune investment [19]. The evidence is transcriptional and

physiological rather than a direct demonstration that immune expenditure causes a specific lifespan reduction. Maintenance costs must therefore be attached to measured functions rather than inferred from theory alone.

Reproductive tissues themselves can be maintenance-intensive. In honey-bee queens, variation in stored-sperm viability was negatively associated with the abundance of particular immune proteins in spermathecal fluid [20]. In *Lasius niger* queens, immune activation reduced stored-sperm viability in established queens but not equivalently in incipient queens [21]. Together, these studies indicate that a putative reproduction-maintenance cost can depend on adult state and the tissue or function examined. They do not justify a constant immune-versus-reproduction exchange rate across insects.

Long-lived social insects further challenge a single antagonistic model. In *Macrotermes bellicosus*, reproductive and worker castes differed in age-associated transposon-defense patterns, linking exceptional reproductive longevity with caste-specific molecular maintenance signatures [22]. Yet reproductive activation can also accompany stronger stress resistance: honey-bee workers activated reproductively showed increased resistance to abiotic and biotic stress [23]. In *Temnothorax rugatulus*, fertile worker states were associated with extended longevity and physiological changes that were at least partly plastic under altered social conditions [24]. These results are not evidence that reproduction generally improves maintenance. They show that social state can reorganize the relationship between fertility, protection, and survival.

Cross-species molecular comparisons reinforce the need for restraint. Comparative transcriptomics across termites, bees, and ants found limited universality in ageing- and fecundity-associated expression, with substantial dependence on taxon, caste, tissue, and downstream process [25]. In *Cryptotermes secundus*, a queen-associated coexpression network was identified, but experimental endocrine manipulation did not support every inferred component of the proposed regulatory explanation [26]. Molecular covariance and network topology must therefore remain distinct from validated causal pathways.

For this article, maintenance cost is best treated as a vector of function-specific demands rather than a scalar. Immune defense, reproductive-tissue preservation, genome defense, proteostasis, stress resistance, and other maintenance processes may move together, oppose one another, or change sign across reproductive states. The proposed synthesis is that adult longevity becomes interpretable only after specifying which maintenance functions are being preserved and what evidence connects them to survival.

Because these cross-scale patterns are difficult to compare in prose without flattening their evidence status, the following grid separates measured maintenance domains from the interpretation they permit and the boundaries they retain.

Table 1. Somatic maintenance costs as state-dependent constraints on interpreting adult longevity

Maintenance dimension or state	Article-specific dimension	Scientific content
Germline–immune allocation	**Biological setting · Evidence**	Adult fruit fly Germline state paired with infection-responsive immune expression
	Consequence for interpreting longevity · Limits and uncertainty	Longer life cannot be assigned to "maintenance" without identifying which defense function changed Expression change does not itself establish survival causation
	Research or test · Evidential standing	Pair immune function, reproductive state, and survival in the same design Evidence-supported pattern
Stored-sperm preservation versus immune activity	**Biological setting · Evidence**	Honey-bee and ant queens Spermathecal protein profiles, sperm viability, immune activation
	Consequence for interpreting longevity · Limits and uncertainty	Reproductive maintenance can itself consume or constrain protective capacity Association and experimental effects differ by species and queen stage
	Research or test · Evidential standing	Measure reproductive-tissue maintenance across adult states Evidence-supported pattern
Caste-linked genome defense	**Biological setting · Evidence**	Termite reproductives and workers Age- and caste-associated transposon-defense expression
	Consequence for interpreting longevity · Limits and uncertainty	Exceptional lifespan may coexist with specialized maintenance architecture Molecular signature is not a proven cause of longevity

	Research or test · Evidential standing	Test candidate defenses experimentally across castes and ages Evidence-supported association
Fertility-linked stress resilience	**Biological setting · Evidence**	Honey-bee workers Reproductive activation paired with abiotic and biotic stress survival
	Consequence for interpreting longevity · Limits and uncertainty	Fertility and maintenance need not be negatively coupled Eusocial worker physiology may not transfer to solitary insects
	Research or test · Evidential standing	Replicate across social states and taxa Evidence-supported counterpattern
Plastic fertile-worker longevity state	**Biological setting · Evidence**	Ant workers Social-state manipulation, fertility, survival, physiological expression
	Consequence for interpreting longevity · Limits and uncertainty	Maintenance allocation can be reorganized by social condition Mechanism and reversibility are system specific
	Research or test · Evidential standing	Follow state transitions with repeated functional measures Evidence-supported pattern
Cross-taxon maintenance heterogeneity	**Biological setting · Evidence**	Termites, bees, and ants Comparative transcriptomic signatures
	Consequence for interpreting longevity · Limits and uncertainty	No single molecular maintenance pathway should be used as a universal longevity proxy Tissue, caste, and species differences remain substantial
	Research or test · Evidential standing	Validate pathway-level claims within rather than across systems first Evidence-supported boundary
Function-specific maintenance vector	**Biological setting · Evidence**	Cross-scale conceptual synthesis Joint interpretation of the preceding evidence classes
	Consequence for interpreting longevity · Limits and uncertainty	"Maintenance cost" should be decomposed into named functions rather than converted into one score No validated universal weighting among functions
	Research or test · Evidential standing	Test whether function-specific maintenance predicts survival independently of reproductive timing and environment Proposed synthesis

Ecological opportunity and mortality context

Adult survival is realized within an environment that determines whether an additional day can be converted into feeding, mating, dispersal, oviposition, parental or colony function, or recovery. Abiotic conditions therefore modify not only mortality risk but also the physiological meaning of persistence. In *Drosophila melanogaster*, ambient temperature altered metabolism and lifespan partly through 4E-BP-dependent physiology [27]. This finding does not establish a universal thermal mechanism for insects, but it demonstrates that longevity measured under one thermal regime cannot automatically be treated as an intrinsic, context-free property.

Natural demographic environments add another layer. Across nine years in wild *G. campestris*, actuarial senescence was slower in years with more female-biased adult sex ratios [28]. The association does not prove that sex ratio alone causes the change, because weather, density, resource conditions, and other annual factors may covary. It nevertheless shows that the apparent rate at which mortality increases with age can shift with the social opportunity environment encountered by adults.

Social exposure can itself alter mortality. Experimental manipulation of neural sexual identity and social composition in *Drosophila* showed that the behavior generated by social partners affected recipient lifespan [29]. Chronological survival is therefore partly produced by interaction structure: two adults with similar intrinsic physiological capacity may face different realized mortality because they inhabit different social environments. Laboratory group composition cannot be assumed to reproduce field social networks, but it establishes the principle that environmental mortality includes biologically generated social exposure.

External hazards can simultaneously reshape survival and reproductive opportunity. In female *Osmia bicornis*, combined sublethal exposure to an insecticide and fungicide reduced longevity and delayed ovarian development under the tested conditions, whereas the corresponding single-compound exposures did not produce the same joint pattern [30]. The important inference is not that chemical mixtures have a universal demographic effect. Rather,

an environmental exposure can change both how long an insect survives and what reproductive opportunities remain within that lifespan.

These observations support a distinction between chronological persistence and opportunity-adjusted persistence. The latter is not a numerical correction. It asks whether the environmental state during surviving days still permits biologically relevant activity. Temperature, sex structure, social interactions, resource availability, and hazards can alter the probability that remaining lifespan contains usable reproductive or functional opportunity. Consequently, a mortality curve should not be interpreted as though every surviving adult-day carries equal biological potential.

The ecological section can be compressed visually only if environmental effects on survival remain separate from the inference that survival retains reproductive or functional value. **Figure 1** therefore places ecological opportunity and mortality exposure on parallel but interacting tracks and makes the laboratory-to-field and evidence-to-proposal boundaries explicit.

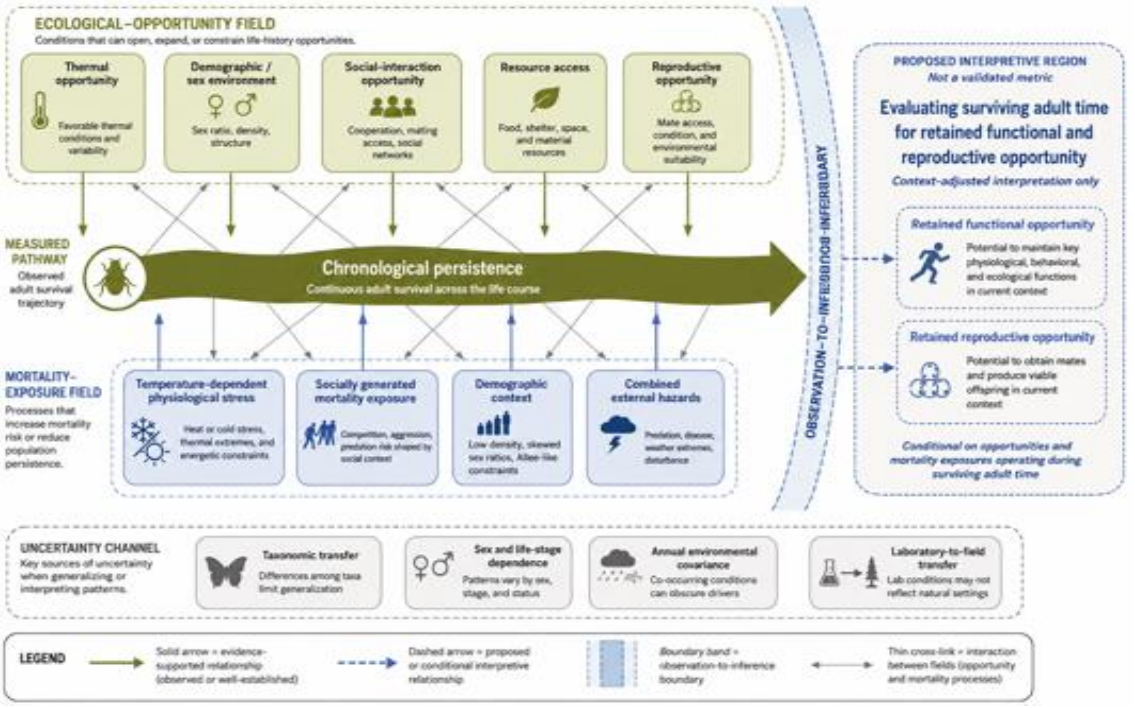


Figure 1. Opportunity windows and mortality filters reshape the biological meaning of adult survival

A context-adjusted interpretation of adult longevity

The evidence assembled here supports neither a rejection of longevity as a useful trait nor a universal replacement metric. Instead, it supports a proposed context-adjusted interpretation in which the meaning of adult survival depends on four distinguishable questions.

First, what persisted? Chronological survival should be separated from the persistence of the function relevant to the hypothesis. Functional measures can accompany lifespan extension, but different functions need not decline at identical rates [10]. Second, when was reproduction realized? Wild-cricket evidence shows that high early reproductive effort need not produce the expected survival cost [13], while experimentally shifted mating conditions can redistribute reproduction across adulthood [14]. Third, what maintenance state supported persistence? Fertility, immunity, stored-sperm preservation, genome defense, and stress resistance cannot be collapsed into a single maintenance currency because their relationships vary among taxa and social states [23]. Fourth, what opportunity remained? Interannual changes in demographic environment can alter observed senescence even within one wild population [28].

These questions generate a conditional rather than additive interpretation. A long-lived adult with maintained function and continuing reproductive opportunity represents a different state from an equally long-lived adult surviving after functional decline or after ecological opportunity has narrowed. Neither state is automatically "better" without specifying the biological question. Likewise, short lifespan produced by high external mortality cannot be interpreted identically to short lifespan produced by rapid intrinsic deterioration.

The proposed framework therefore rejects numerical weighting at this stage. Evidence is insufficient to state that a unit of reproductive delay can be exchanged against a unit of immune maintenance or a day of ecological opportunity. Instead, each dimension acts as an interpretation boundary. **Table 2** specifies the principal failure modes that arise when one or more dimensions are omitted.

Table 2. Failure modes in interpreting adult longevity without reproductive, maintenance, and ecological context

Longevity interpretation scenario	Failure mode or uncertainty	Evidence · Interpretive consequence	Comparative test implication · Evidential standing	Biological setting
Long survival with retained defined function	Unmeasured functions may decline differently	Survival plus system-specific performance Longevity can be interpreted as persistence of both time and measured function	Measure function longitudinally rather than infer it from age Proposed interpretive state	Any taxon with concurrent functional measurement
Long survival after reproductive decline	Future mating or oviposition opportunity may remain incompletely observed	Survival extends beyond major reproductive output Extra days should not automatically be equated with equal residual reproductive value	Report reproductive schedule alongside lifespan Proposed interpretive state	Taxa with age-specific fecundity data
High early reproduction without shortened survival	Condition and ecological opportunity can confound observational patterns	Early reproductive effort plus subsequent survival Absence of a survival cost should be retained rather than forced into a canonical trade-off	Combine effort, condition, environment, and longitudinal survival Evidence-supported failure of a universal rule	Wild or experimentally studied systems where effort is measured
Fertility coupled with enhanced maintenance	Social-insect physiology may be exceptional or state specific	Fertility paired with stress resistance or longevity-associated physiology Reproduction cannot be assumed to oppose maintenance in every state	Test state transitions and solitary-taxon comparators Evidence-supported counterpattern	Eusocial worker or reproductive states
Long survival under narrowed ecological opportunity	Opportunity is difficult to measure directly	Survival persists while mating, resources, movement, or reproductive opportunity decline Chronological persistence may overstate biologically usable adult time	Couple survival with field-relevant opportunity indicators Proposed interpretive state	Environmentally constrained adults
Short survival under high external hazard	Hazard and intrinsic deterioration may be confounded	Mortality elevation with preserved or incompletely measured intrinsic function Short lifespan need not imply rapid intrinsic senescence	Estimate environmental mortality separately where feasible Proposed interpretive state	Field or exposure-driven context
Cross-species lifespan ranking without matched context	Taxonomic and measurement non-equivalence	Species-level lifespan summaries Ranking can conflate reproductive schedule, social system, maintenance biology, and mortality environment	Harmonize life-history and ecological covariates before inference Proposed methodological warning	Comparative datasets

The central implication is that adult longevity should be treated as an interpretable coordinate, not a self-sufficient verdict on life-history performance. The same number of surviving days can arise from slower functional deterioration, altered reproduction, specialized maintenance, social protection, benign environmental conditions, or reduced external hazard. Evidence from wild insects is particularly important because annual ecological variation changes the observed expression of senescence [3].

This interpretation also changes how classical trade-offs should be used. Failure to detect a reproduction-survival cost in ant queens or wild crickets does not invalidate allocation theory; it limits the claim that the trade-off must be visible as reduced adult lifespan under all conditions [5]. Nutrient-specific allocation in *Drosophila* similarly shows that the apparent cost of reproduction can depend on which limiting resource is measured [15]. Eusocial systems add an even stronger boundary: reproductive activation may accompany enhanced stress resistance rather

than reduced maintenance [23]. A useful theory of adult longevity must therefore allow negative, null, and positive reproduction-maintenance relationships without treating any one pattern as universal.

The evidence base remains taxonomically uneven. *Drosophila* contributes unusually detailed genetic and nutritional evidence, while Hymenoptera and termites provide important social-insect counterexamples. Wild longitudinal evidence is much rarer, and cross-species transcriptomic work shows that ageing-associated molecular signatures are not uniformly conserved across social insects [25]. Consequently, the proposed context-adjusted interpretation should not be represented as an empirically validated pan-insect model.

Mechanistic validation and ecological validation also require different evidence. A coexpression network can generate a plausible mechanistic hypothesis yet fail a targeted endocrine manipulation [26]. Conversely, a robust field association between demographic conditions and senescence can remain mechanistically unresolved [28]. Future work should retain this separation rather than treating molecular detail as automatically superior evidence of ecological consequence.

Implications for comparative life-history studies

Comparative studies should report adult lifespan together with the temporal distribution of reproduction whenever feasible. Age at first and peak reproduction, late-life reproductive persistence, and the interval between reproductive decline and death can reveal differences hidden by lifetime totals. This is especially important when selection or experimental evolution directly modifies reproductive timing [9].

Functional lifespan should likewise be defined by the biological system under study. Locomotion, flight, immune competence, stress resistance, reproductive-tissue integrity, and other traits are not interchangeable measures of "health." Their relevance depends on sex, life stage, social state, and ecology. Comparative designs should therefore identify the functional endpoint before interpreting longer survival as preserved organismal performance.

Finally, ecological opportunity should accompany cross-species or cross-population longevity comparisons whenever adequate data exist. Thermal environment, demographic structure, social exposure, food availability, and external hazards can modify both mortality and the opportunity to reproduce. When these variables cannot be measured, the appropriate response is not to impute them but to state explicitly that the biological meaning of observed longevity remains only partly resolved.

A strong test of the proposed framework would measure survival, age-specific reproduction, at least one pre-specified functional domain, relevant maintenance processes, and mortality context within the same populations across multiple environments or years. Such studies could determine whether context-adjusted interpretation improves biological explanation without assuming in advance that a universal weighting scheme exists.

Conclusion

Adult longevity is biologically informative, but elapsed survival alone cannot reveal what persisted, when reproduction occurred, what maintenance supported persistence, or whether ecological conditions still allowed surviving adults to convert time into biological opportunity. The evidence considered here shows that these dimensions can diverge and that reproduction-maintenance relationships can be negative, absent, positive, or strongly context dependent.

The proposed context-adjusted interpretation therefore treats chronological lifespan, functional persistence, reproductive timing, maintenance state, and ecological opportunity as distinct but interacting dimensions. It is not a score and is not presented as a validated predictor of fitness. Its purpose is narrower: to prevent equivalent numbers of adult days from being interpreted as equivalent biological states when the supporting life-history context differs.

Comparative validation across orders, sexes, social systems, and natural environments is now needed. Until such evidence exists, the strongest inference is conditional: adult longevity gains meaning when the reproductive, physiological, and ecological circumstances of those surviving days are known.

Acknowledgments: None

Conflict of Interest: None

Financial Support: None

Ethics Statement: None

References

1. Flatt T. Life-history evolution and the genetics of fitness components in Drosophila melanogaster. Genetics. 2020;214(1):3-48. doi:10.1534/genetics.119.300160
2. Zajitschek F, Zajitschek SRK, Bonduriansky R. Senescence in wild insects: key questions and challenges. Funct Ecol. 2020;34(1):26-37. doi:10.1111/1365-2435.13399
3. Rodríguez-Muñoz R, Boonekamp JJ, Liu XP, Skicko I, Haugland Pedersen S, Fisher DN, et al. Comparing individual and population measures of senescence across 10 years in a wild insect population. Evolution. 2019;73(2):293-302. doi:10.1111/evo.13674
4. Blacher P, Huggins TJ, Bourke AFG. Evolution of ageing, costs of reproduction and the fecundity-longevity trade-off in eusocial insects. Proc Biol Sci. 2017;284(1858):20170380. doi:10.1098/rspb.2017.0380
5. Schrempf A, Giehr J, Röhrl R, Steigleder S, Heinze J. Royal Darwinian demons: enforced changes in reproductive efforts do not affect the life expectancy of ant queens. Am Nat. 2017;189(4):436-42. doi:10.1086/691000
6. Jehan C, Sabarly C, Rigaud T, Moret Y. Late-life reproduction in an insect: Terminal investment, reproductive restraint or senescence. J Anim Ecol. 2021;90(1):282-97. doi:10.1111/1365-2656.13367
7. Zandveld J, van den Heuvel J, Mulder M, Brakefield PM, Kirkwood TBL, Shanley DP, et al. Pervasive gene expression responses to a fluctuating diet in Drosophila melanogaster: The importance of measuring multiple traits to decouple potential mediators of life span and reproduction. Evolution. 2017;71(11):2572-83. doi:10.1111/evo.13327
8. Hoedjes KM, Rodrigues MA, Flatt T. Amino acid modulation of lifespan and reproduction in Drosophila. Curr Opin Insect Sci. 2017;23:118-22. doi:10.1016/j.cois.2017.07.005
9. Hoedjes KM, van den Heuvel J, Kapun M, Keller L, Flatt T, Zwaan BJ. Distinct genomic signals of lifespan and life history evolution in response to postponed reproduction and larval diet in Drosophila. Evol Lett. 2019;3(6):598-609. doi:10.1002/evl3.143
10. Parkhitko AA, Wang L, Filine E, Jouandin P, Leshchiner D, Binari R, et al. A genetic model of methionine restriction extends Drosophila health- and lifespan. Proc Natl Acad Sci U S A. 2021;118(40):e2110387118. doi:10.1073/pnas.2110387118
11. Ngian ZK, Lin WQ, Ong CT. NELF-A controls Drosophila healthspan by regulating heat-shock protein-mediated cellular protection and heterochromatin maintenance. Aging Cell. 2021;20(5):e13348. doi:10.1111/acel.13348
12. Everman ER, Morgan TJ. Antagonistic pleiotropy and mutation accumulation contribute to age-related decline in stress response. Evolution. 2018;72(2):303-17. doi:10.1111/evo.13408
13. Rodríguez-Muñoz R, Boonekamp JJ, Liu XP, Skicko I, Fisher DN, Hopwood P, et al. Testing the effect of early-life reproductive effort on age-related decline in a wild insect. Evolution. 2019;73(2):317-28. doi:10.1111/evo.13679
14. Filice DCS, Bhargava R, Dukas R. Plasticity in male mating behavior modulates female life history in fruit flies. Evolution. 2020;74(2):365-76. doi:10.1111/evo.13926
15. Zanco B, Mirth CK, Sgrò CM, Piper MDW. A dietary sterol trade-off determines lifespan responses to dietary restriction in Drosophila melanogaster females. Elife. 2021;10:e62335. doi:10.7554/eLife.62335
16. Savola E, Montgomery C, Waldron FM, Monteith KM, Vale P, Walling C. Testing evolutionary explanations for the lifespan benefit of dietary restriction in fruit flies (Drosophila melanogaster). Evolution. 2021;75(2):450-63. doi:10.1111/evo.14146
17. Niitepõld K. Effects of flight and food stress on energetics, reproduction, and lifespan in the butterfly Melitaea cinxia. Oecologia. 2019;191(2):271-83. doi:10.1007/s00442-019-04489-8
18. Almond EJ, Huggins TJ, Crowther LP, Parker JD, Bourke AFG. Queen longevity and fecundity affect conflict with workers over resource inheritance in a social insect. Am Nat. 2019;193(2):256-66. doi:10.1086/701299

19. Rodrigues MA, Merckelbach A, Durmaz E, Kerdaffrec E, Flatt T. Transcriptomic evidence for a trade-off between germline proliferation and immunity in Drosophila. Evol Lett. 2021;5(6):644-56. doi:10.1002/evl3.261
20. McAfee A, Chapman A, Pettis JS, Foster LJ, Tarpy DR. Trade-offs between sperm viability and immune protein expression in honey bee queens (Apis mellifera). Commun Biol. 2021;4(1):48. doi:10.1038/s42003-020-01586-w
21. Chérasse S, Aron S. Impact of immune activation on stored sperm viability in ant queens. Proc Biol Sci. 2018;285(1893):20182248. doi:10.1098/rspb.2018.2248
22. Elsner D, Meusemann K, Korb J. Longevity and transposon defense, the case of termite reproductives. Proc Natl Acad Sci U S A. 2018;115(21):5504-9. doi:10.1073/pnas.1804046115
23. Kennedy A, Herman J, Rueppell O. Reproductive activation in honeybee (Apis mellifera) workers protects against abiotic and biotic stress. Philos Trans R Soc Lond B Biol Sci. 2021;376(1823):20190737. doi:10.1098/rstb.2019.0737
24. Negroni MA, Macit MN, Stoldt M, Feldmeyer B, Foitzik S. Molecular regulation of lifespan extension in fertile ant workers. Philos Trans R Soc Lond B Biol Sci. 2021;376(1823):20190736. doi:10.1098/rstb.2019.0736
25. Korb J, Meusemann K, Aumer D, Bernadou A, Elsner D, Feldmeyer B, et al. Comparative transcriptomic analysis of the mechanisms underpinning ageing and fecundity in social insects. Philos Trans R Soc Lond B Biol Sci. 2021;376(1823):20190728. doi:10.1098/rstb.2019.0728
26. Lin S, Werle J, Korb J. Transcriptomic analyses of the termite, Cryptotermes secundus, reveal a gene network underlying a long lifespan and high fecundity. Commun Biol. 2021;4:384. doi:10.1038/s42003-021-01892-x
27. Carvalho GB, Drago I, Hoxha S, Yamada R, Mahneva O, Bruce KD, et al. The 4E-BP growth pathway regulates the effect of ambient temperature on Drosophila metabolism and lifespan. Proc Natl Acad Sci U S A. 2017;114(36):9737-42. doi:10.1073/pnas.1618994114
28. Rodríguez-Muñoz R, Boonekamp JJ, Fisher D, Hopwood P, Tregenza T. Slower senescence in a wild insect population in years with a more female-biased sex ratio. Proc Biol Sci. 2019;286(1900):20190286. doi:10.1098/rspb.2019.0286
29. Flintham EO, Yoshida T, Smith S, Pavlou HJ, Goodwin SF, Carazo P, et al. Interactions between the sexual identity of the nervous system and the social environment mediate lifespan in Drosophila melanogaster. Proc Biol Sci. 2018;285(1892):20181450. doi:10.1098/rspb.2018.1450
30. Sgolastra F, Arnan X, Cabbri R, Isani G, Medrzycki P, Teper D, et al. Combined exposure to sublethal concentrations of an insecticide and a fungicide affect feeding, ovary development and longevity in a solitary bee. Proc Biol Sci. 2018;285(1885):20180887. doi:10.1098/rspb.2018.088