Avian epigenetic clocks: state of the art and call to action

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Abstract

DNA methylation-based epigenetic clocks are powerful biomarkers of chronological and biological age, estimating age from CpG-specific methylation patterns that integrate developmental history, environmental exposure, physiological stress, and stochastic epigenetic change. Despite rapid advances in mammals, avian epigenetic clocks remain scarce, limiting comparative inference and our understanding of how ageing varies across ecological and evolutionary contexts. Here, we review existing avian epigenetic clocks and evaluate their performance for age estimation and biological inference. We argue that birds provide a uniquely powerful system for resolving what epigenetic age represents, due to unique qualities such as external embryonic development, rapid postnatal growth, long-term field studies, and nucleated erythrocytes that enable minimally invasive longitudinal sampling. Together with variation in lifespan and life-history strategies, and expanding genomic and physiological resources, these features position birds as an ideal system for linking developmental environments to epigenetic ageing trajectories. We conclude that integrating epigenetic clocks into avian research will improve age estimation, demographic inference, and conservation applications, while enabling mechanistic tests of how development, environment, and physiology shape ageing. We call for expansion of publicly available DNA methylation datasets from known-age individuals across the avian tree of life, alongside standardized and reproducible analytical workflows to fully realise this potential.

Keywords: epigenetic clock, bird, life-history evolution, ageing, development

Why birds matter for epigenetic ageing research

Birds are increasingly recognized as powerful systems for the study of ageing (Harper & Holmes, 2021). Many species live substantially longer than expected for their body size despite high metabolic rates, elevated body temperatures, and other physiological traits associated with accelerated ageing in mammals (Austad, 2011; Holmes & Ottinger, 2003; Travin & Feniouk, 2016). This pattern challenges pace-of-life theory and suggests the evolution of enhanced somatic maintenance and delayed senescence mechanisms, shaped in part by reduced extrinsic mortality associated with flight (Austad & Fischer, 1991; Ricklefs, 2010). Avian cells also often exhibit increased resistance to oxidative stress and other cytoprotective adaptations (Castiglione et al., 2020; Harper & Holmes, 2021), while work on telomeres, neurogenesis, and dietary interventions has established birds as key models of ageing and resilience (Barnea & Pravosudov, 2011; Wilbourn et al., 2018). Combined with experimental tractability and long-term ecological datasets, their exceptional longevity for their size makes birds particularly attractive systems for emerging biomarkers of biological ageing. Despite these advantages, a major challenge remains: accurately quantifying both chronological age and biological ageing in wild and experimental populations.

Epigenetic clocks are statistical models that estimate age and ageing-related phenotypes from DNA methylation (DNAm) at selected CpG sites (Horvath, 2013). The earliest “first-generation” clocks were trained to provide highly accurate age estimates across humans and other vertebrates (Horvath & Raj, 2018; Tangili et al., 2023). More recent approaches, mainly in mammals, incorporate outcomes like lifespan, mortality risk, or physiological decline, capturing components of biological ageing and providing biomarkers that

respond to health interventions (“second-generation” clocks; see Levine et al., 2018; Lu et al., 2019). Although still rarely applied in wild systems, these models are increasingly used to quantify “age acceleration” (Horvath et al., 2014) and link DNAm patterns to environmental or experimental perturbations. While many clocks are species- or tissue-specific, some show striking evolutionary conservation, including pan-mammalian models that predict age across 185 species (Lu et al., 2023). To date, most clock development has occurred in humans and laboratory model organisms, providing strong methodological foundations but limited insight into how ageing varies in natural populations. Only recently have epigenetic clocks been applied more broadly to wild animals, where they are beginning to reveal how environmental factors can shift epigenetic age estimates and produce measurable age acceleration (Anderson et al., 2021; Pinho et al., 2022; Sullivan et al., 2022; Zipple et al., 2025).

Epigenetic clock literature closely links biological ageing to growth and developmental processes (Gibson et al., 2019), yet the mammalian systems that form the foundation of this field provide limited access to the early-life environments (i.e., the womb) in which epigenetic signatures are established. Although valuable long-term wild mammal datasets exist (e.g., Soay sheep: Catchpole et al., 2000; Yellowstone Wolves: Charruau et al., 2016; Amboseli Baboons: Tung et al., 2016), they are largely “hands-off,” relying on infrequent, minimally invasive sampling with limited resolution during early development and little opportunity to capture fine-scale longitudinal change. Laboratory mice allow controlled access to development but under highly simplified environmental conditions, whereas human cohorts are typically late-life biased, clinically enriched, and rarely cover the full lifespan. As a result, a central limitation of mammalian systems is the

inability to resolve how early-life programming shapes ageing trajectories, highlighting a key need for models that capture epigenetic dynamics from the earliest stages of life under ecologically realistic conditions.

Birds provide a unique opportunity to overcome many of these limitations. Unlike mammals, avian development occurs outside the mother, allowing direct observation and manipulation of developmental environments through incubation and brood-size manipulations, cross-fostering, and other interventions during the very periods when epigenetic signatures are first established. In many species, the widespread use of nest boxes further enhances experimental tractability by providing repeated access to individuals and allowing fine-scale manipulation of early-life. Rapid post-hatching growth, during which nestlings can double in mass within days (Tangili, Briga, et al., 2026), extends this experimental window well beyond embryonic development. In addition, ringing nestlings soon after hatching enables many long-term avian study systems (e.g., Florida scrub-jay: Fox et al., 2006; Seychelles warbler: Hammers et al., 2015; Common guillemot: Reed et al., 2008) to generate known-age individuals with detailed developmental, survival, and reproductive histories. By combining experimental tractability with ecological realism, birds provide a powerful framework for disentangling developmental, environmental, and ageing-related sources of DNAm variation across diverse life-history strategies and lifespans. Birds may therefore offer a rare opportunity to experimentally investigate the developmental origins of biological ageing and track their consequences across the lifespan.

Despite their promise, birds remain under-represented in epigenetic clock research (Tangili et al., 2023), with validated clocks currently available for only a handful of species

(Table 1; Cristofari et al., 2026; De Paoli-Iseppi et al., 2019; Gerber et al., 2025; Haller et al., 2025; Raddatz et al., 2021). This gap is striking given the complementary strengths of avian systems and epigenetic clocks. Birds offer exceptional opportunities to address fundamental unresolved questions in epigenetic ageing research, particularly how developmental environments, ecological conditions, and life-history strategies shape epigenetic ageing trajectories. Conversely, epigenetic clocks have clear potential to transform avian research by enabling high-resolution age estimation, demographic inference, conservation applications, and the study of ageing in natural populations. Here, we review emerging literature on avian epigenetic clocks, highlight opportunities across ecology, evolution, and conservation, and identify priorities for future research.

Avian epigenetic clocks as a proof of concept

Epigenetic clocks have now been developed to predict chronological age for several avian species using approaches ranging from targeted to whole-genome methylation sequencing (Table 1, Cristofari et al., 2026; De Paoli-Iseppi et al., 2019; Gerber et al., 2025; Haller et al., 2025; Raddatz et al., 2021). Although avian clock development remains limited compared to mammals, existing clocks collectively demonstrate that age-associated DNAm signatures are detectable across avian taxa and life histories.

Across these avian epigenetic clocks, median absolute deviations (deviation between predicted and actual age) are small in absolute terms, ranging from ~1 day to ~2.5 years (Table 1). Scaled to maximum lifespan, these values suggest remarkably high accuracy: ~0.03% in domestic chickens (~3.4 days of a ~30-year lifespan), ~0.05% in chestnut-crowned babblers, ~2–3% in great tits, and up to ~9% in king penguins (~2.5 years of a

27-year lifespan). However, these estimates can overstate performance because many clocks are trained using relatively narrow age ranges, often focused on early development. When prediction error is evaluated relative to the training age window rather than maximum lifespan, accuracy declines substantially;- for example, prediction error in chicken approaches ~10% across individuals aged 3-35 days. Thus, these clocks should be interpreted within the contexts for which they were constructed rather than as broadly transferable measures of age. Nevertheless, epigenetic clocks often provide substantially finer age resolution than traditional approaches based on morphological traits such as plumage characteristics, body size, or wing length, which are frequently coarse, stage-dependent, and unreliable beyond early life.

Beyond chronological age estimates, emerging evidence suggests avian epigenetic clocks may also capture biologically meaningful variation. In great tits, rapid postnatal growth induced by brood size reduction was associated with epigenetic age acceleration, linking early-life growth dynamics to DNAm ageing trajectories (Haller et al., 2025). In king penguins, captive individuals exhibited higher epigenetic age acceleration than wild ones, potentially reflecting changes in growth, metabolic, and cardiac-related pathways (Cristofari et al., 2026). In chickens, experimentally-induced inflammation alters epigenetic ageing profiles, implicating immune activation and physiological stress in modulating DNAm age estimates (Raddatz et al., 2021). Together, these findings suggest that epigenetic age may be shaped not only by chronological time but also variation in growth, energetic state, and physiological stress. Future development of second-generation avian clocks will improve these signals, enabling more direct assessment of biological ageing phenotypes.Despite the limited number of avian clocks, broader

evidence from DNAm studies suggests that perturbations could alter epigenetic age acceleration (Ruuskanen, 2024). Exposure to toxicants such as arsenic and lead alters DNAm near growth-related genes such as *IGF2BP1* (Laine et al., 2021; Mäkinen et al., 2022). Likewise, variation in incubation temperature, brood size, and hormone production produces lasting epigenetic changes in genes linked to development, metabolism, behaviour, and cognition (Corbett et al., 2020; Karami et al., 2025; Sepers et al., 2024, 2025; Tangili et al., 2026a; Y. Wang et al., 2019). Social and ecological conditions further reinforce these patterns: solitary rearing affects DNAm of cancer-related genes in chickens (Pertille et al., 2017; Pértille et al., 2020), while urban environments are associated with methylation of metabolic pathways (von Holdt et al., 2023; Watson et al., 2021). Because DNAm can regulate gene expression (Kilvitis et al., 2019; Laine et al., 2016; Lindner et al., 2021; Vinoth et al., 2018), these shifts likely have physiological consequences. Collectively, these effects converge on genes involved in development, metabolism, immunity, and stress regulation - the same functional domains enriched in epigenetic ageing clocks (Gibson et al., 2019; Li et al., 2025; Lu et al., 2023).

Together, these findings suggest that epigenetic clocks may be capturing more than chronological time: they likely reflect a structured combination of developmental programming, environmental exposure, and physiological state, all acting on the same gene networks that underpin ageing-related DNAm change. Even though avian epigenetic clocks remain largely at a proof-of-concept stage, available evidence highlights their considerable promise. Collectively, this positions avian epigenetic clocks as a framework for linking molecular, ecological, and evolutionary perspectives on ageing.

Table 1. Information on the experimental design, methods for DNA methylation extraction and validation approaches used to develop the existing avian epigenetic clocks (N=5). Species-specific maximum lifespan information was derived from the AnAge database (https://genomics.senescence.info/species/index.html).

Reference	Species	Wild or Captive	Tissue	Maximum Lifespan (years)	Age Range	Sample Size	Method	R^2	MAD	Validation Approach
De Paoli-Iseppi et al. 2019	Short-tailed shearwater (*Ardenna tenuirostris*)	wild	blood	38	0-21 years	42	DREAM	0.587	-	Elastic net
Raddatz et al. 2021	Domestic chicken (*Gallus gallus domesticus*)	captive	muscle, ileum, jejunum, spleen	30	3-35 days	36	WGBS	-	3.4 days (RMSE)	Elastic net
Haller et al. 2025	Great tit (*Parus major*)	wild	blood	15.4	Development clock:6-15 days, Ageing clock:0.-6 years	Development clock:67, Ageing clock:122	epiGBS	Development clock:0.792, Ageing clock: 0.706	Development clock:1.06 days, Ageing clock: 0.4 years	Elastic net
Gerber et al 2025	chestnut-crowned babbler (*Pomatostomus ruficeps*)	wild	blood	8.3	0-19 days	56	EM-seq	0.903	1.6 days	Elastic net
Cristofari et al. 2026	King peguin (*Aptenodytes patagonicus*)	both	blood	27	1-38 years	64	EM-Seq	0.91	2.48 years (RMSE)	Elastic net

Leveraging avian epigenetic clocks to study ageing

Mechanistic interpretations of epigenetic age. A central challenge in epigenetic clock research is determining whether epigenetic age plays a causal or correlative role in ageing. These clocks integrate signals from development, environmental exposures, and stochastic epigenetic drift. One hypothesis views epigenetic ageing as the accumulation of stochastic errors in DNAm maintenance and gradual loss of epigenomic information. An alternative model proposes that epigenetic age reflects persistence of early-life gene-regulatory programmes, implying that ageing partly represents an extension of developmental trajectories. Other frameworks emphasise progressive failure of chromatin maintenance or interpret DNAm changes as integrative records of cumulative physiological stressors (Bell et al., 2019; Horvath & Raj, 2018).

Resolving these alternatives requires moving from prediction to causal inference, through targeted perturbation of epigenetic states (e.g. genome editing or partial reprogramming) to test whether modifying clock-associated DNAm alters ageing trajectories (Nakamura et al., 2021). This should be combined with longitudinal, multi-tissue and multi-omics sampling, integrated with measures of DNA damage, proteostasis, mitochondrial function, and immune ageing. Longitudinal designs are particularly important for distinguishing within-individual trajectories from population-level patterns, while comparative analyses across species can identify conserved links between methylation dynamics, lifespan, metabolism, and developmental timing.

Within this framework, birds provide a uniquely informative but underutilised system. External embryonic development enables direct access to early gene-regulatory processes, allowing tests of whether epigenetic clocks originate in developmental

programmes or emerge later from damage accumulation. In birds, nucleated erythrocytes and broadly tissue-general DNAm patterns (Lindner, Verhagen, Viitaniemi, Laine, Visser, Husby, & Van Oers, 2021) support the use of minimally invasive blood sampling for clock development. These strengths are complemented by expanding genomic resources and established physiological tools for linking DNAm to organismal function. However, birds currently lag behind mammals in genetic toolkits: while avian CRISPR, primordial germ cell manipulation, and in ovo electroporation can be implemented in poultry, they remain less efficient and scalable than mammalian conditional genetic systems (Cooper et al., 2018; Williams et al., 2018). Despite this, birds occupy a complementary niche linking epigenetic clocks to developmental architecture and life-history evolution, while mammals remain optimal for precise causal dissection of ageing mechanisms.

Early-life environments and the developmental origins of ageing. Birds are uniquely powerful systems for experimental manipulation of early-life conditions through brood size manipulations, nutritional supplementation, and thermal or hormonal challenges, allowing direct tests of how developmental environments shape lifelong phenotypes (Barker, 2004; Gluckman & Hanson, 2004). Such manipulations influence survival, reproduction, and senescence (Cooper and Kruuk, 2018; Monaghan, 2008; Wada & Coutts, 2021), yet the mechanisms linking early conditions to ageing trajectories remain poorly resolved. Across vertebrates, early-life adversity can leave persistent biological signatures, including telomere attrition and reduced lifespan (Boonekamp et al., 2014; Heidinger et al., 2012; Nettle et al., 2013) while in humans, it is associated with accelerated epigenetic ageing and elevated disease and mortality risk later in life (Huang et al., 2019; Levine et al., 2018; Marioni et al., 2015; Schlomer, 2024; Tehranifar et al., 2013). Because DNAm mediates developmental

programming, epigenetic clocks provide a high-resolution framework for linking early environments to later-life biological ageing . In birds, known hatch dates, repeated sampling, and long-term fitness records enable direct tests of whether early-life conditions induce persistent epigenetic signatures that predict survival, reproduction, and senescence. More broadly, epigenetic clocks offer a mechanistic bridge between developmental plasticity and life history evolution.

Comparative life-history evolution. Birds exhibit exceptional variation in lifespan (Wasser & Sherman, 2010) and pace-of-life strategies, providing a natural framework for comparative ageing research. This diversity raises a central question for epigenetic clock research: do age-associated DNAm changes represent conserved molecular signatures of ageing, or are they systematically shaped by evolved life-history strategies across species? Cross-species analyses can test whether DNAm ageing patterns are conserved across avian lineages or scale predictably with maximum lifespan, as observed in mammals (Bertucci-Richter & Parrott, 2023; Li et al., 2024; Mayne et al., 2019). Similar macroevolutionary structure is evident in other ageing traits, including telomere dynamics, which covary with lifespan across birds (Tangili et al., 2026; Tricola et al., 2018), suggesting that ageing biomarkers may reflect both conserved biological processes and evolved differences in life-history strategy.

These considerations motivate a pan-avian epigenetic clock framework: a standardized comparative methylation system enabling direct alignment of DNAm ageing trajectories across species. Such a framework would allow researchers to disentangle whether exceptional longevity arises from uniformly slower epigenetic ageing, shifts in specific DNAm trajectories, or enhanced epigenetic maintenance mechanisms operating across lineages, and whether life-history strategies are

encoded in shared or divergent epigenetic signatures. However, progress is constrained by a key methodological limitation. Most mammalian epigenetic clocks rely on standardized platforms such as the HorvathMammalMethylChip40 (Arneson et al., 2022), which targets ~37,000 conserved CpG sites and enables robust cross-species comparisons (Lu et al., 2023). The absence of an equivalent avian platform limits comparability across species and hinders the development of truly comparative epigenetic ageing models. Developing a conserved avian CpG panel or analogous standardized sequencing framework would therefore be a critical step toward pan-avian epigenetic clock construction and evolutionary inference.

Sex differences in longevity and ageing rates. Sex differences in lifespan and ageing rates add an important layer of biological complexity for epigenetic clock design. In birds, females are the heterogametic sex (ZW) and often exhibit shorter lifespans than males (Tower & Arbeitman, 2009), consistent with broader evidence that the homogametic sex tends to live longer across taxa (Xirocostas et al., 2020). Although the study of sex chromosome DNAm in relation to ageing is still in its infancy, evidence is emerging both in humans and birds. In humans, hypermethylation of Y-linked CpGs has been linked to mortality risk (Lund et al., 2020), while there are only a few X-linked CpG sites whose DNAm significantly changes with age (Acevedo et al., 2015). Most recently, X and Y chromosome dosage has been found to influence epigenetic aging (Zhang et al., 2025). In birds, many age-related CpGs are found on sex chromosomes, suggesting a potential contribution to sex-specific ageing trajectories and longevity (Tangili et al., 2025). Birds therefore offer a powerful comparative system for disentangling the role of sex chromosome methylation in ageing, given their contrasting ZW system relative to mammalian XY sex determination. These findings highlight that sex chromosomes should not be excluded

from (avian) epigenetic clock construction, and that explicitly modeling sex-linked variation may improve age prediction and better capture biologically meaningful differences in ageing and lifespan.

Applications of avian epigenetic clocks in ecology and conservation

Chronological age estimation for demography and population ecology. Many ecological studies rely on minimum age categories unless individuals are followed from hatching or exhibit clear age-specific morphology. Once validated in independent datasets, epigenetic clocks enable continuous age estimation from cross-sectional samples, allowing population age structure, age-specific survival, recruitment, and reproductive output to be inferred without decades of intensive monitoring (e.g., Eichenberger et al., 2026; Heydenrych et al., 2021; Roman et al., 2024). Compared to categorical approaches (e.g., “second-year” vs “after-second-year”), they provide higher-resolution age estimates that may reveal late-life demographic patterns such as actuarial senescence and terminal investment, which are often difficult to detect in wild systems (Nussey et al., 2013). Incorporating clock-derived ages into capture-mark-recapture or integrated population models could reduce bias from unknown age at first capture, a longstanding challenge in estimating age-specific survival and senescence (Gaillard & Lemaître, 2020; Lebreton et al., 1992; Schaub & Abadi, 2011). In addition, clocks enable age estimation in underrepresented classes, including juveniles, floaters, and non-breeders, improving inference on full population structure. Clocks further allow rapid detection of demographic shifts following environmental change and retrospective analysis of archived samples (Eichenberger et al., 2026). More broadly, epigenetic clocks transform age from a latent demographic variable to

a directly measurable trait, enabling stronger tests of age-structured ecological and evolutionary theory in the wild.

Health, disease, welfare, and livestock. In agricultural mammals, epigenetic biomarkers are increasingly being explored as tools to evaluate health, welfare, and production efficiency (Clarke et al., 2021; Hayes et al., 2021), with potential applications in selective breeding for robustness and longevity (Wang and Ibeagha-Awemu, 2021). Although poultry-specific applications remain in their early stages, intensive production systems may be especially well suited for these approaches given their rapid turnover and high economic sensitivity to variation in performance and health. Poultry are exposed to chronic stressors, including high stocking densities, controlled photoperiods, strong artificial selection for rapid growth, alongside routine immunological and veterinary interventions (Ncho et al., 2025). These conditions can induce sustained inflammatory and metabolic changes that are likely to be reflected in DNAm dynamics (Pértille et al., 2020; Raddatz et al., 2021; Ratan et al., 2023). In this context, epigenetic age acceleration may serve as an integrative biomarker of cumulative physiological burden, capturing trade-offs between productivity and somatic maintenance in systems where selection for growth and feed efficiency may come at the expense of long-term physiological robustness.

Conservation and wildlife management. Reliable age estimation has substantial conservation value (Hutchinson, 1991), yet this information is often unavailable for threatened bird populations due to the difficulty of long-term individual monitoring. Epigenetic clocks offer a non-lethal means of estimating age from routine biological samples, enabling reconstruction of population age structure and improved estimation of survival, recruitment, and population viability. Beyond this, epigenetic age estimates

could improve captive breeding, translocation, and reintroduction programmes by identifying age distributions among breeders and evaluating whether released individuals represent appropriate demographic cohorts. Similar molecular ageing approaches have already been suggested for use in fisheries and wildlife management (Anastasiadi et al., 2026; Newediuk et al., 2025), supporting the feasibility of age-based inference in applied conservation contexts. Archived tissues and museum collections further extend this framework by enabling retrospective reconstruction of demographic change and environmental impacts over time. Together, epigenetic clocks provide a scalable link between individual biological ageing and population-level conservation decision-making.

A call to action

Avian epigenetic clocks are evolving from proof-of-concept biomarkers to practical tools for quantifying biological age, ageing trajectories, and environmental effects in wild and captive bird populations. However, current models are largely restricted to a small number of species and first-generation designs, with limited integration of experimental manipulations, fitness outcomes, or environmental drivers of ageing. As a result, it remains unclear whether they capture true variation in ageing rate, plastic physiological state, or statistical structure in methylation data. Birds offer a uniquely powerful system for resolving these questions due to their exceptional diversity in lifespan, life-history strategies, and environmental exposures, combined with rich long-term ecological datasets and experimental tractability. Realising this potential will require a coordinated shift toward a comparative, pan-avian framework built on (i) known-age longitudinal datasets, (ii) standardized methylation profiling and clock calibration, and (iii) explicit links between epigenetic age, survival, and fitness.

Advancing this field will require coordinated community action, particularly the development of shared, open-source analytical pipelines for methylation processing, model training, and validation. Standardization of these models - comparable to those that have driven progress in mammalian systems - will reduce methodological heterogeneity and enable robust cross-study and cross-species comparisons. We therefore call for a community-wide commitment to data sharing and methodological transparency, with the goal of generating comparable, high-quality methylation datasets across diverse avian systems. With these foundations, avian biologists will not only adopt epigenetic clocks and use them as tools, but actively shape their conceptual development, establishing birds alongside mammals as a core system for understanding the universal processes shaping the biology of ageing.

BOX 1. Open questions in the study of epigenetic clocks in ecology and evolution

The applications mentioned in this manuscript raise a set of fundamental questions that directly connect back to the interpretative framework outlined earlier, particularly the distinction between true ageing trajectories, statistical association, and adaptive plasticity.

1. What do epigenetic clocks actually measure? Do they reflect causal components of biological ageing, downstream consequences of ageing, or mere correlates of developmental and environmental history?

2. Are clock-associated CpGs mechanistically involved in ageing? Are age-informative loci enriched in conserved regulatory pathways governing growth, development, maintenance, immune function, or stress responses in birds?

3. Stability and causality of early-life effects. Do developmental DNAm changes persist to shape adult ageing trajectories, and are such effects adaptive, neutral, or deleterious in the long term?

4. Tissue and organismal relevance. How well does avian blood DNAm capture systemic ageing processes, and does tissue choice alter inferred relationships between epigenetic age and fitness?

5. Population and environmental modulation. To what extent do local environments, social systems, and life-history variation alter clock performance, and how much inter-population variation reflects biology versus methodological artefacts?

6. Limits of transferability and generalisability. Under what conditions can clocks be used across species or populations, and what minimal calibration is required to correct systematic bias?

7. Fitness and survival prediction. Can epigenetic clocks be extended from age estimation to prediction of survival, reproductive senescence, or remaining lifespan in non-model species populations, analogous to human second-generation epigenetic clocks?

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