

Social organisation predicts lifespan in mammals

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Abstract

1. Recent comparative analyses have identified positive associations between social organisation and longevity in mammals, but independent replication with larger datasets is needed to establish the robustness of this pattern.
2. Here, we analysed maximum recorded lifespan, body mass, and social organisation data for 1,436 mammal species using Bayesian phylogenetic comparative methods, confirming that group-living and pair-living species exhibit longer lifespans than solitary species after controlling for body mass and phylogeny.
3. Pair-living species showed slightly longer lifespans than group-living species (though credible intervals overlapped), while body mass slopes did not differ substantially among social categories and activity period showed weak associations with lifespan.
4. These results provide independent corroboration of recent findings linking sociality to longevity in mammals and suggest that while group living may reduce predation risk, pathogen transmission costs in larger groups may constrain longevity benefits.
5. Our findings, based on the largest comparative dataset analysed to date, strengthen the evidence that social organisation is a key factor shaping mammalian life history evolution alongside body size and ecological adaptations.

Introduction

Understanding variation in maximum lifespan among mammals has long engaged evolutionary biologists, as it reflects adaptations shaped by ecological and life-history factors. Extrinsic mortality, largely driven by predation, imposes strong selective pressures on ageing and longevity (Williams, 1957; Reznick et al., 2004). Body size is perhaps the most important factor: larger mammals generally face fewer predators, allowing them to allocate more resources to maintenance and repair, thereby extending their lifespans. In addition to body size, adaptations that reduce predation, such as protective shells, burrowing, or flight, also lower extrinsic mortality, contributing to the evolution of longer lifespans (Healy et al., 2014). Comparative analyses of bats and marsupials similarly support reduced environmental vulnerability as a driver of longer lifespan, rather than simple rate-of-living predictions (Austad & Fischer, 1991). Furthermore, lifespan is correlated with other traits, including age at maturity and parental investment, consistent with the disposable soma theory, which highlights the trade-off between energy allocation for reproduction and cellular repair. Increasingly, behavioural factors such as sociality are recognised for their impact on lifespan dynamics, adding another dimension to our understanding of longevity evolution (Zhu et al., 2023).

Social groups protect their members from predation and starvation (Alexander, 1974; Clutton-Brock, 2002; Wrangham, 1980). Reduced risk of death from such extrinsic causes is expected to promote the evolution of longer lifespans (Lucas & Keller, 2019; Stearns, 1992; P. D. Williams & Day, 2003). According to evolutionary theories of senescence, a lower rate of extrinsic mortality increases average life expectancy, thereby conferring an adaptive advantage to slow life histories characterised by long lifespans and repeated reproduction (Hamilton, 1966; Medawar, 1952; G. C. Williams, 1957). Although this idea has been criticised (Abrams, 1993; Moorad et al., 2019), it is broadly supported by empirical data (Gaillard & Lemaître, 2017). For instance, among mammals, the

ability to fly - an effective strategy to avoid predation - is associated with increased lifespan (Healy et al., 2014). Since group living similarly aids predator avoidance, resource defence, and foraging efficiency, we might expect a positive relationship between group living and lifespan in comparative analyses; this logic is consistent with selfish-herd theory, in which individuals reduce their domain of danger by moving towards conspecifics (Hamilton, 1971). However, a broad-scale quantitative study of 253 mammalian species failed to detect this relationship (Kamilar et al., 2010). To investigate this unexpected lack of support, we present a re-analysis of the topic, expanding the sample size to include a greater diversity of mammal species.

To assess whether sociality and longevity correlate, it is first essential to define sociality. Previous studies, such as Kamilar et al. (2010), quantified sociality by examining the median group size for each species and tested whether larger group sizes correlate with lifespan in mammals. However, animal social systems are diverse, ranging from anonymous aggregations to highly cooperative, stable groups of familiar, frequently interacting individuals. These systems also vary widely in group size (from pairs to thousands) and cohesion (from temporary to permanent associations). Each social structure likely represents an evolutionarily stable strategy, adapted to a species' specific ecological and life-history contexts. This perspective also recognises that group living involves trade-offs, including costs such as food and reproductive competition, increased within-group conflict, higher risk of disease transmission, and greater visibility to predators. Consequently, while small groups may offer optimal fitness benefits for some species, larger groups may better optimise fitness in others, depending on ecological and predation pressures. This variability raises the question of whether adding an additional group member would have a consistent, additive, linear effect on reducing extrinsic mortality across all mammal species, thereby increasing lifespan. Thus, Kamilar et al.'s (2010) conclusion that sociality does not correlate with longevity in mammals may be premature. To address this question, we re-examined the relationship using a larger dataset. In this

analysis, we coded social systems as a categorical variable with three levels - solitary, pair-living, and group-living (Lukas & Clutton-Brock, 2013) - to capture the broader diversity of mammalian social structures and their potential impacts on longevity.

Recently, Zhu et al. (2023) reported a positive association between group-living and longevity across ~1,000 mammal species, using the categorical social organisation framework of Lukas and Clutton-Brock (2013) and integrating comparative transcriptomics to identify molecular pathways underlying this relationship. Their study represents a major advance in demonstrating that social organisation predicts longevity when measured appropriately. However, independent replication with different datasets and analytical implementations is essential to establish the robustness of macroevolutionary patterns, particularly given potential sensitivities to phylogenetic trees, lifespan data sources, and species sampling. Here, we provide such an independent analysis using a larger dataset of 1,436 mammal species.

Lifespan tends to increase with body mass, and larger species generally outlive smaller ones due to a range of interconnected biological and ecological factors, many of which influence extrinsic mortality risk. Perhaps most importantly, larger animals tend to face fewer natural predators, reducing their exposure to extrinsic mortality risk and shifting optimal life-history strategies towards somatic maintenance to support longer-term survival. Accompanying these longer-term prospects is a related shift towards a slower life history, including fewer offspring, delayed reproduction, and extended parental care, aligning with their capacity for repeated reproduction over a longer period. Additionally, larger animals typically have slower metabolic rates, which further contribute to extended lifespans by reducing cellular turnover and oxidative damage. Recognising the importance of extrinsic mortality risk, our analysis controls for body mass to isolate the potential effect of

sociality on lifespan, examining whether sociality further enhances longevity beyond what body size alone would predict.

Another trait often assumed to reduce predation risk and, therefore, expected to be associated with long lifespans is nocturnality. Nocturnal species face only predators that can hunt in darkness (Kronfeld-Schor & Dayan, 2003). According to the nocturnal bottleneck hypothesis, early eutherian mammals were strictly nocturnal, avoiding interspecific competition and predation by diurnal reptiles (Gerkema et al., 2013). Reconstructions of primate evolution support the co-evolution of sociality with a shift in activity pattern from nocturnal to diurnal (Gerkema et al., 2013; Shultz et al., 2011). Sociality may have provided the necessary protection from predation to enable activity during daylight. A previous study found that mammalian lifespans did not differ by activity period (Healy et al., 2014). To check whether Healy et al.'s result rests on an undetected interaction between activity period and sociality, we reanalysed the original data, adding information on social organisation, to ask whether diurnality may be associated with lower lifespans, but only in solitary species.

To shed new light on whether group living has led to the evolution of longer lifespans by reducing extrinsic mortality, we analysed data on maximum lifespan, body mass, and sociality for 1,436 mammal species. We also added data on the activity period for 611 species. To correct for shared evolutionary history, we used a Bayesian approach following the procedure developed by Healy et al. (2014). Using this approach, we address three predictions. Firstly, we predict that group-living species will have longer lifespans than pair-living species, which, in turn, will have longer lifespans than solitary species. Secondly, we expect that body size affects lifespan differently in social and non-social species. Specifically, we expect non-social species to gain a greater lifespan benefit from increased body size than social species, which may instead rely on group living as an adaptive strategy for predator defence. Finally, we expect diurnal species to generally have shorter lifespans

than nocturnal species. However, for diurnal, group-living species, the risk of predation is likely mitigated through mechanisms associated with group living, such as dilution, predator confusion, and collective vigilance (Cresswell & Quinn, 2011; Sword et al., 2005), potentially resulting in lifespans comparable to those of nocturnal species of similar body mass.

Methods

Social organisation, activity period, and maximum recorded lifespan data

We used three published databases (Healy et al., 2014; Lukas & Clutton-Brock, 2013; Myhrvold et al., 2015), hereafter referred to as the Healy, Lukas, and Myhrvold databases, respectively. The Lukas database, extracted from the appendix of Lukas and Clutton-Brock (2013), categorises the social organisation of 2,454 mammal species. Specifically, it classifies species as solitary, socially monogamous (hereafter, pair-living; where one adult male and one female form a pair), or group-living. This classification is based on adult home-range use, with the refinement that singular cooperative breeders (where non-breeding offspring provide alloparental care) are considered pair-living. Details of data sources and categorisation criteria are provided in Lukas & Clutton-Brock (2013).

Life history data were sourced from the Myhrvold database, a publicly accessible repository of amniote life history traits (see Myhrvold et al., 2015 for more information). We extracted two key variables: maximum recorded lifespan (hereafter 'maximum lifespan') and adult body mass.

Maximum lifespan is regarded as a measure of the pace of life (*sensu* Baudisch, 2011) because it is highly correlated with life expectancy from maturity. As an extreme-value statistic, maximum lifespan is sensitive to population sample size (N). However, as Finch and Pike (1996) noted, the influence of N on maximum lifespan diminishes logarithmically under Gompertz mortality

conditions, and maximum lifespan is more influenced by variation in the Gompertz rate parameter than by N. Although sexual size dimorphism is frequently observed in mammals, our databases typically record the weight of the larger sex. Given the vast range of weight data across species (from 2 grams to 4 tons), variation between sexes within a species is minor in comparison. Thus, we are confident in using a single species-specific measure in our analysis. Finally, we obtained data on the species' activity period (diurnal, crepuscular, nocturnal or cathemeral) from Healy et al. (2014).

Phylogeny and taxonomy

We integrated the three datasets described above with a fourth dataset containing phylogenetic information used for phylogenetic correction. Rather than using a single phylogenetic tree, we used an approach developed by Healy et al. (2014) that accounts for the inherent uncertainty in phylogenetic tree topology and dating by using multiple trees, treating them as a Bayesian posterior distribution. Specifically, we used 25 trees sampled from the full set of 101 trees provided by Kuhn et al. (2011), each representing a distinct resolution of polytomies from the 'best dates' mammalian supertree phylogeny published by Bininda-Emonds et al. (2007). We obtained unique species identifiers and updated the trees to reflect the synonymisations recognised by the Integrated Taxonomic Information System (ITIS). We refer to our tree data hereafter as the Kuhn data.

Our taxonomic framework was based on ITIS (www.itis.gov, ITIS 2016), which assigns unique, persistent identifiers, known as Taxonomic Serial Numbers (TSNs), to scientific names. These TSNs were crucial for our analysis. Using the **taxize** R package (Chamberlain et al., 2020), we retrieved TSNs for each species across the Lukas, Myhrvold, Healy, and Kuhn datasets with the **get_tsn** function. When the function returned no TSN, we flagged the species, checked for typographical errors, corrected them, and reran **get_tsn**. For multiple potential matches, we selected the TSN of

the valid species. Despite this systematic approach, some species remained unmatched, and we manually reviewed them to identify possible synonyms not listed in ITIS.

Because TSNs may correspond to synonyms rather than valid species names, we used the **synonyms** function in **taxize** to retrieve accepted TSNs, thereby consolidating duplicate entries into a single valid species record. In the Lukas dataset, we confirmed that social organisation information remained consistent across merged species. For the Myhrvold dataset, the longest recorded lifespan among merged records was taken as the maximum recorded lifespan. Unused tips were pruned from the phylogenetic trees using the **ape** package (Paradis & Schliep, 2019). This rigorous procedure produced four harmonised datasets, confidently aligned using accepted TSNs. We then filtered the integrated dataset to include only species with complete data on the variables of interest: lifespan and sociality, or lifespan, sociality, and activity period. We also excluded all volant (flying) and gliding mammal species. The final dataset comprised 1,436 mammal species from 516 genera and 23 orders, with body masses ranging from 2.33 g (the Shrew species, *Suncus etruscus*, *S. fellowesgordoni* and *S. bosei*) to 4,630 kg (the African Forest Elephant, *Loxodonta cyclotis*). For analyses involving activity periods, we restricted our sample to 611 species classified as either nocturnal or diurnal in the Healy dataset that matched records in the Lukas dataset.

Statistical analysis

We examined associations between social organisation, body mass, and maximum recorded lifespan (MRLS) using Bayesian phylogenetic mixed models implemented in the MulTree R package (v1.3.7; Guillaume & Healy, 2014), which builds on MCMCglmm (Hadfield et al., 2010). These models account for phylogenetic non-independence by including a random effect for phylogeny and incorporate phylogenetic uncertainty by fitting each model across multiple plausible trees rather than a single consensus tree.

Before analysis, we log-transformed (natural logarithm) the maximum recorded lifespan and adult body mass. Body mass was converted from grams to kilograms before transformation. Social organisation was modelled as a three-level factor (solitary, pair-living, group-living). For activity analyses, the activity period was represented either as the full factor (diurnal, nocturnal, cathemeral, crepuscular) or, in a focused subset, as a two-level factor (nocturnal, diurnal).

We fitted a candidate set of models that varied in fixed-effect structure and data subset (Table 1).

The primary inferential models reported in the main text were: (i) additive sociality model ($\text{MRLS} \sim \text{wt} + \text{socialOrg}$), (ii) sociality-by-body-mass interaction model ($\text{MRLS} \sim \text{wt} * \text{socialOrg}$), and (iii) sociality-by-activity interaction model in the nocturnal/diurnal subset ($\text{MRLS} \sim \text{wt} + \text{socialOrg} * \text{activityPeriod}$). Additional candidate models, including quadratic terms for body mass and alternative activity formulations, were used for sensitivity analyses and are reported in the Supporting Information.

We ran model MCMCs for 12,000 iterations with a burn-in of 2,000 and thinning of 20, using 4 parallel chains. Following Healy et al. (2014), we used inverse-Wishart priors with $V = 0.5$ and $\nu = 0.002$ for residual and phylogenetic random effects. We evaluated convergence using Gelman-Rubin potential scale reduction factors (PSRF; threshold < 1.1) and effective sample size diagnostics across all fitted models and trees (Supporting Information).

We conducted all analyses in R (R Core Team, 2026) using the recorded platform shown in the reproducibility output.

Results

Social organisation and lifespan

In the additive sociality model, pair-living and group-living species ('social species') had longer lifespans than solitary species at comparable body mass, and pair-living and group-living species showed no clear difference (Figure 1; Table 2). In the interaction model, the body-mass-by-sociality interaction terms were weak, and their credible intervals overlapped zero, indicating limited evidence that body-mass slopes differ strongly among social categories (Figure 2; Table 3). We therefore report both additive and interaction formulations as complementary views of the same relationship.

Quadratic sensitivity analyses (adding wt^2 terms) did not materially alter the inference about social organisation effects; these model outputs are reported in the Supporting Information (Tables S1-S2).

Social organisation, activity period, and lifespan

In the nocturnal/diurnal subset, evidence for activity-period effects was weaker than for sociality and body mass (Figure 3; Table 4). Activity main effects and sociality-by-activity interaction terms generally had credible intervals that overlapped zero, so these patterns should be interpreted with caution.

Discussion

Independent confirmation of sociality-longevity associations

Our results provide independent confirmation that social organisation predicts maximum recorded lifespan in mammals, after accounting for body mass and phylogeny. Analysing 1,436 species - the largest dataset examined to date - we found that pair-living and group-living species both had longer lifespans than solitary species, with no clear difference between the pair-living and group-living

categories. These findings corroborate the recent transcriptomic and comparative study by Zhu et al. (2023), which reported similar patterns across ~1,000 mammalian species using the same categorical social organisation framework as that of Lukas and Clutton-Brock (2013).

The convergence of results across independent datasets, analytical implementations, and sample compositions strengthens confidence that the sociality-longevity association is robust and not an artefact of specific methodological choices. While Zhu et al. (2023) found no significant difference between pair-living and solitary species in their phylogenetic ANOVA, their MCMCglmm results aligned with ours, showing that both pair-living and group-living species lived longer than solitary species. Our larger sample size (1,436 vs 974 species) may provide greater power to detect the pair-living effect, although differences in phylogenetic trees, lifespan data sources, and species composition may also contribute to this subtle divergence. Resolving whether pair-living consistently confers longevity benefits beyond solitary living will require examining which taxonomic groups and ecological contexts drive this signal.

Why group-living doesn't dramatically outlive pair-living: pathogen trade-offs

A striking finding common to both our study and Zhu et al. (2023) is that group-living species do not have substantially longer lifespans than pair-living species, despite theoretical expectations that larger groups provide greater predator dilution, confusion effects, and collective vigilance (Cresswell & Quinn, 2011; Sword et al., 2005). This pattern suggests that group size may yield diminishing or even negative marginal returns on longevity beyond the pair-living state.

One plausible explanation is that pathogen transmission costs rise with group size and density, offsetting the predation benefits of larger groups. Zhu et al.'s (2023) transcriptomic analysis provides molecular support for this trade-off: they identified immunity-related genes and pathways that were upregulated in group-living species, potentially reflecting evolved immune defences against elevated

pathogen exposure in denser social aggregations. Social organisation strongly shapes parasite transmission dynamics (Altizer et al., 2003). Group-living species experience higher contact rates and closer proximity among individuals, creating favourable conditions for infectious disease spread.

The observation that pair-living species achieve longevity comparable to that of group-living species may thus reflect an optimal balance: pairs provide sufficient social benefits - two individuals enable cooperative vigilance, resource defence, and mutual support - without incurring the elevated disease risks of larger groups. This interpretation aligns with life-history theory emphasising trade-offs in social evolution (Lucas & Keller, 2019) and suggests that the longevity benefits of sociality may saturate or plateau beyond relatively small group sizes, at least across broad comparative scales.

Categorical social organisation reveals patterns missed by group size

Our findings, together with those of Zhu et al. (2023), demonstrate the value of modelling social organisation as a categorical trait (solitary, pair-living, group-living) rather than as a continuous measure of group size. Kamilar et al. (2010) found no relationship between median group size and longevity across 253 mammal species, leading to the conclusion that sociality does not predict longevity. However, both our study and Zhu et al. detect clear associations using the categorical approach pioneered by Lukas and Clutton-Brock (2013).

This methodological advance likely succeeds because it captures qualitative differences in social structure that continuous group size obscures. The transition from solitary to pair-living represents a fundamental shift in social organisation - the formation of long-term social bonds, coordinated activity budgets, and sustained interaction between individuals. Similarly, the transition from pair-living to group-living entails new social dynamics, including within-group competition, dominance hierarchies, and multi-individual cooperation. These structural differences may have distinct selective consequences for longevity that are not well captured by the number of group members alone.

Moreover, group size varies enormously even within the “group-living” category (from small family groups of 3-5 to herds of hundreds), and this variation likely reflects diverse ecological and demographic pressures that do not uniformly affect longevity.

Body mass, activity period, and the scope of social effects.

We found limited evidence that body size affects lifespan differently in social versus solitary species. The body-mass-by-sociality interaction terms in our models were weak, with credible intervals overlapping zero, suggesting that social benefits to longevity operate relatively consistently across the mammalian size spectrum. This contrasts with our prediction that solitary species might gain greater longevity benefits from increased body size (via reduced predation) than social species that rely on group-based defences. The lack of a clear interaction may indicate that body size and sociality influence longevity through partially independent mechanisms, or that our comparative approach lacks power to detect size-dependent social effects.

Our analyses of activity period yielded weaker, more uncertain results than those for body mass and social organisation. In the nocturnal/diurnal subset (611 species), activity period main effects and sociality-by-activity interactions generally had credible intervals that overlapped zero. This null result is noteworthy given predictions from the nocturnal bottleneck hypothesis (Gerkema et al., 2013) and the idea that diurnal species face higher predation risk without social protection. The absence of clear activity effects suggests either that diurnal and nocturnal predation pressures are more balanced than assumed, or that activity period interacts with sociality and longevity in more complex, context-dependent ways that our broad comparative models do not capture. Zhu et al. (2023) controlled for activity period in their models but did not test interactions; our focused examination confirms that activity period does not strongly modulate the sociality-longevity relationship across mammals.

Mechanisms and macroevolutionary patterns: integrating comparative and molecular approaches

While our phylogenetic comparative approach establishes the sociality-longevity association at the macroevolutionary scale, Zhu et al.'s (2023) transcriptomic analysis provides crucial mechanistic insights. They identified immune-related and hormonal pathways whose expression correlates with both social organisation and longevity, with particularly striking evidence that group-living species experience relaxed selection on longevity-related genes while solitary species show intensified selection. This molecular signature complements our macroevolutionary findings and suggests a feedback loop: social environments enable longer lifespans by reducing extrinsic mortality, which in turn relaxes selection on cellular longevity mechanisms. Future work should test specific mechanistic hypotheses integrating comparative patterns with molecular data - for example, whether immunity gene expression predicts longevity more strongly in group-living than solitary species, or whether hormonal stress markers mediate social bond quality and individual lifespan within species.

Limitations and future directions

Our comparative models identify associations but cannot establish causation. Social organisation, longevity, and other life-history traits coevolve in response to complex ecological and demographic factors, and distinguishing cause from consequence requires further evidence. Experimental manipulations are rarely feasible at macroevolutionary scales, but within-species comparisons - examining populations or individuals that vary in sociality - can provide complementary causal insights (Archie et al., 2014; Silk et al., 2010). Similarly, our categorical classification of social organisation, while an improvement over continuous group size, still obscures substantial variation within categories. The “group-living” category encompasses diverse social systems, from loosely

associated herds to tightly bonded cooperative groups, and these subtypes likely differ in their consequences for longevity.

Maximum recorded lifespan, our response variable, has well-known limitations as an extreme-value statistic sensitive to sample size and study effort (Finch & Pike, 1996). If social species are better studied than solitary species, this could inflate apparent longevity differences. However, the concordance of results across multiple datasets and analytical methods suggests that ascertainment bias is unlikely to fully explain the observed patterns. Future comparative work should explicitly incorporate ecological moderators of the sociality-longevity relationship, including predation regime, habitat structure, disease prevalence, and resource predictability. These factors likely determine when and why social organisation enhances longevity. Additionally, finer-scale phylogenetic analyses within well-studied clades (e.g., primates, carnivores, ungulates), where social organisation is characterised in greater detail, could reveal whether specific social features - cooperative breeding, stable bonds, kin structure - drive longevity effects. Finally, integrating comparative genomics, transcriptomics, and epigenomics with demographic and behavioural data from long-term field studies will be essential for identifying the proximate mechanisms linking social environments to extended healthspan and lifespan.

Conclusions

Our analysis of 1,436 mammal species provides robust, independent confirmation that social organisation predicts longevity, even after controlling for body mass and phylogeny. Together with recent molecular evidence (Zhu et al., 2023), these findings confirm that the evolution of sociality and extended lifespan are correlated across the mammalian phylogeny. The pattern appears to reflect reduced extrinsic mortality in social species, although pathogen-transmission costs may limit the longevity advantages of large groups relative to pairs. These results contribute to a growing

understanding of sociality as a key life-history trait that, alongside body size and ecological specialisations, shapes the extraordinary diversity of ageing and longevity strategies across mammals.

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Data availability

All data and code required to reproduce this study are archived on Zenodo:

<https://doi.org/10.5281/zenodo.18665209>.

References

- Abrams, P. A. (1993). Does increased mortality favor the evolution of more rapid senescence? *Evolution*, 47(3), 877–887. <https://doi.org/10.1111/j.1558-5646.1993.tb01241.x>
- Alexander, R. D. (1974). The Evolution of Social Behavior. *Annual Review of Ecology and Systematics*, 5, 325–383. <https://doi.org/10.1146/annurev.es.05.110174.001545>
- Altizer, S., Nunn, C. L., Thrall, P. H., Gittleman, J. L., Antonovics, J., Cunningham, A. A., Dobson, A. P., Ezenwa, V., Jones, K. E., Pedersen, A. B., Poss, M., & Pulliam, J. R. C. (2003). Social organization and parasite risk in mammals: Integrating theory and empirical studies. *Annual Review of Ecology, Evolution, and Systematics*, 34, 517–547. <https://doi.org/10.1146/annurev.ecolsys.34.030102.151725>
- Archie, E. A., Tung, J., Clark, M., Altmann, J., & Alberts, S. C. (2014). Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proceedings of the Royal Society B*, 281(1793), 20141261. <https://doi.org/10.1098/rspb.2014.1261>
- Austad, S. N., & Fischer, K. E. (1991). Mammalian Aging, Metabolism, and Ecology: Evidence From the Bats and Marsupials. *Journal of Gerontology*, 46, B47–B53. <https://doi.org/10.1093/geronj/46.2.B47>
- Baudisch, A. (2011). The pace and shape of ageing. *Methods in Ecology and Evolution*, 2(4), 375–382. <https://doi.org/10.1111/j.2041-210X.2010.00087.x>
- Bininda-Emonds, O. R. P., Cardillo, M., Jones, K. E., MacPhee, R. D. E., Beck, R. M. D., Grenyer, R., ... Purvis, A. (2007). The delayed rise of present-day mammals. *Nature*, 446(7135), 507–512. <https://doi.org/10.1038/nature05634>

- Chamberlain, S., Szoecs, E., Foster, Z., Arendsee, Z., Boettiger, C., Ram, K., Bartomeus, I., Baumgartner, J., O'Donnell, J., Oksanen, J., Greshake Tzovaras, B., Marchand, P., Tran, V., Salmon, M., Li, G., & Grenié, M. (2020). *taxize: Taxonomic information from around the web* (R package version 0.9.98). <https://doi.org/10.32614/CRAN.package.taxize>
- Clutton-Brock, T. (2002). Breeding together: kin selection and mutualism in cooperative vertebrates. *Science*, 296(5565), 69–72. <https://doi.org/10.1126/science.296.5565.69>
- Cresswell, W., & Quinn, J. L. (2011). Predicting the optimal prey group size from predator hunting behaviour. *Journal of Animal Ecology*, 80(2), 310–319. <https://doi.org/10.1111/j.1365-2656.2010.01775.x>
- Finch, C. E., & Pike, M. C. (1996). Maximum life span predictions from the Gompertz mortality model. *The Journals of Gerontology. Series A, Biological Sciences and Medical Sciences*, 51(3), B183–B194. <https://doi.org/10.1093/gerona/51A.3.B183>
- Gaillard, J.-M., & Lemaître, J.-F. (2017). The Williams' legacy: A critical reappraisal of his nine predictions about the evolution of senescence. *Evolution; International Journal of Organic Evolution*, 71(12), 2768–2785. <https://doi.org/10.1111/evo.13379>
- Gerkema, M. P., Davies, W. I. L., Foster, R. G., Menaker, M., & Hut, R. A. (2013). The nocturnal bottleneck and the evolution of activity patterns in mammals. *Proceedings. Biological Sciences / The Royal Society*, 280(1765), 20130508. <https://doi.org/10.1098/rspb.2013.0508>
- Guillerme, T., & Healy, K. (2014, November). *mulTree: a package for running MCMCglmm analysis on multiple trees*. Zenodo. <https://doi.org/10.5281/zenodo.12902>

Hadfield, J. D., & Others. (2010). MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software*, 33(2), 1–22.

<https://doi.org/10.18637/jss.v033.i02>

Hamilton, W. D. (1966). The moulding of senescence by natural selection. *Journal of Theoretical Biology*, 12(1), 12–45. [https://doi.org/10.1016/0022-5193\(66\)90184-6](https://doi.org/10.1016/0022-5193(66)90184-6)

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, 31(2), 295–311. [https://doi.org/10.1016/0022-5193\(71\)90189-5](https://doi.org/10.1016/0022-5193(71)90189-5)

Healy, K., Guillaume, T., Finlay, S., Kane, A., Kelly, S. B. A., McClean, D., ... Cooper, N. (2014). Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proceedings of the Royal Society, Series B*, 281(1784), 20140298. <https://doi.org/10.1098/rspb.2014.0298>

Kamilar, J. M., Bribiescas, R. G., & Bradley, B. J. (2010). Is group size related to longevity in mammals? *Biology Letters*, 6(6), 736–739. <https://doi.org/10.1098/rsbl.2010.0348>

Kronfeld-Schor, N., & Dayan, T. (2003). Partitioning of time as an ecological resource. *Annual Review of Ecology, Evolution, and Systematics*, 34, 153–181.

<https://doi.org/10.1146/annurev.ecolsys.34.011802.132435>

Kuhn, T. S., Mooers, A. Ø., & Thomas, G. H. (2011). A simple polytomy resolver for dated phylogenies. *Methods in Ecology and Evolution*, 2(5), 427–436. <https://doi.org/10.1111/j.2041-210X.2011.00103.x>

Lucas, E. R., & Keller, L. (2019). The co-evolution of longevity and social life. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.13445>

Lukas, D., & Clutton-Brock, T. H. (2013). The evolution of social monogamy in mammals. *Science*, 341(6145), 526–530. <https://doi.org/10.1126/science.1238677>

Medawar, P. B. (1952). *An Unsolved Problem of Biology*. London: Routledge.

Moorad, J., Promislow, D., & Silvertown, J. (2019). Evolutionary ecology of senescence and a reassessment of Williams’ “extrinsic mortality” hypothesis. *Trends in Ecology & Evolution*, 34(6), 519–530. <https://doi.org/10.1016/j.tree.2019.02.006>

Myhrvold, N. P., Baldridge, E., Chan, B., Sivam, D., Freeman, D. L., & Ernest, S. K. M. (2015). An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles: Ecological Archives E096-269. *Ecology*, 96(11), 3109–3109. <https://doi.org/10.1890/15-0846.1>

Paradis, E., & Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35, 526–528. <https://doi.org/10.1093/bioinformatics/bty633>

R Core Team. (2026). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>

Reznick, D. N., Bryant, M. J., Roff, D., Ghalambor, C. K., & Ghalambor, D. E. (2004). Effect of extrinsic mortality on the evolution of senescence in guppies. *Nature*, 431, 1095–1099. <https://doi.org/10.1038/nature02936>

Zhu, P., Liu, W., Zhang, X. et al. (2023). Correlated evolution of social organization and lifespan in mammals. *Nature Communications*, 14, 372. <https://doi.org/10.1038/s41467-023-35869-7>

Shultz, S., Opie, C., & Atkinson, Q. D. (2011). Stepwise evolution of stable sociality in primates. *Nature*, 479(7372), 219–222. <https://doi.org/10.1038/nature10601>

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, 20(15), 1359–1361. <https://doi.org/10.1016/j.cub.2010.05.067>

Stearns, S. C. (1992). *The Evolution of Life Histories*. Oxford University Press.

Sword, G. A., Lorch, P. D., & Gwynne, D. T. (2005). Insect behaviour: migratory bands give crickets protection. *Nature*, 433(7027), 703. <https://doi.org/10.1038/433703a>

Williams, G. C. (1957). Pleiotropy, natural selection, and the evolution of senescence. *Evolution; International Journal of Organic Evolution*, 11(4), 398–411. <https://doi.org/10.1111/j.1558-5646.1957.tb02911.x>

Williams, P. D., & Day, T. (2003). Antagonistic pleiotropy, mortality source interactions, and the evolutionary theory of senescence. *Evolution; International Journal of Organic Evolution*, 57(7), 1478–1488. <https://doi.org/10.1111/j.0014-3820.2003.tb00356.x>

Wrangham, R. W. (1980). An Ecological Model of Female-Bonded Primate Groups. *Behaviour*, 75, 262–300. <https://doi.org/10.1163/156853980X00447>

Figures

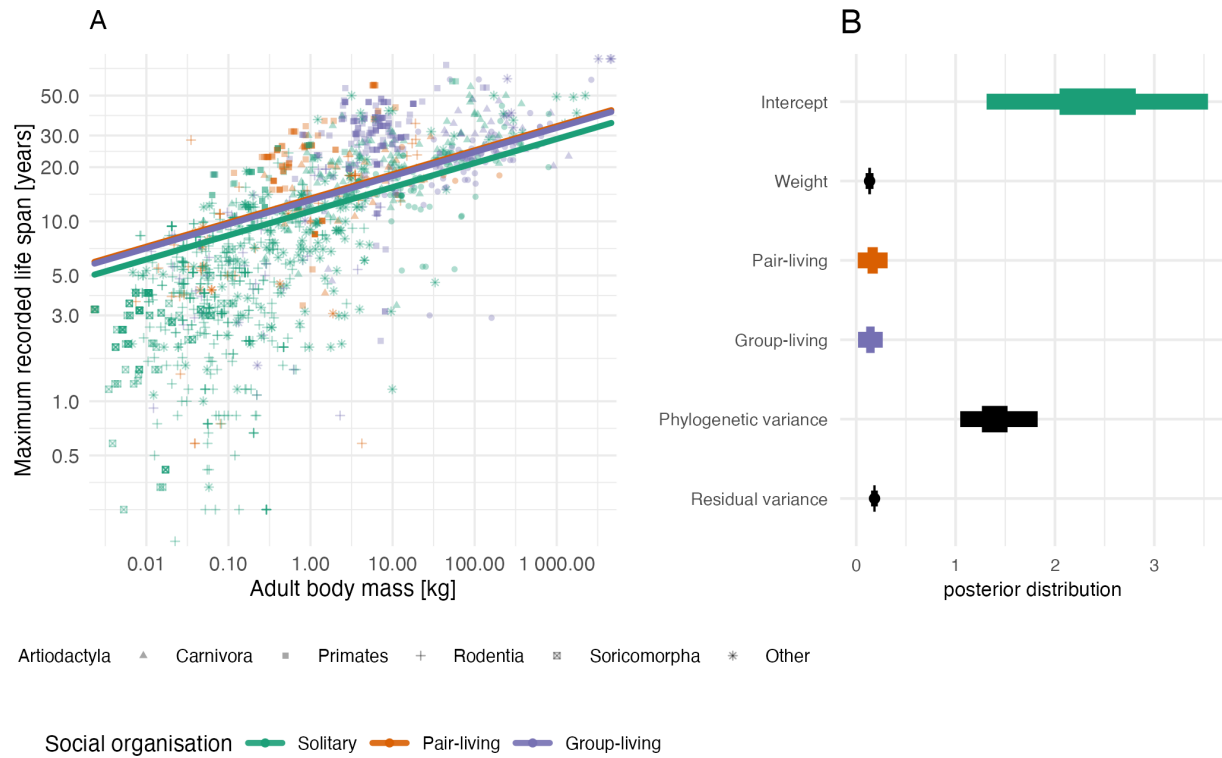


Figure 1. Additive model ($mrls \sim wt + socialOrg$) for 1,436 mammal species. Panel A shows observed maximum lifespan versus adult body mass (both on log scales): points are species, point colour indicates social organisation (solitary, pair-living, group-living), and point shape indicates order (top five orders shown separately; all others grouped as Other). Solid lines are model predictions using posterior modal estimates for each social category. Panel B shows posterior summaries for model coefficients: point = mode, thick bar = 50% credible interval, thin bar = 95% credible interval.

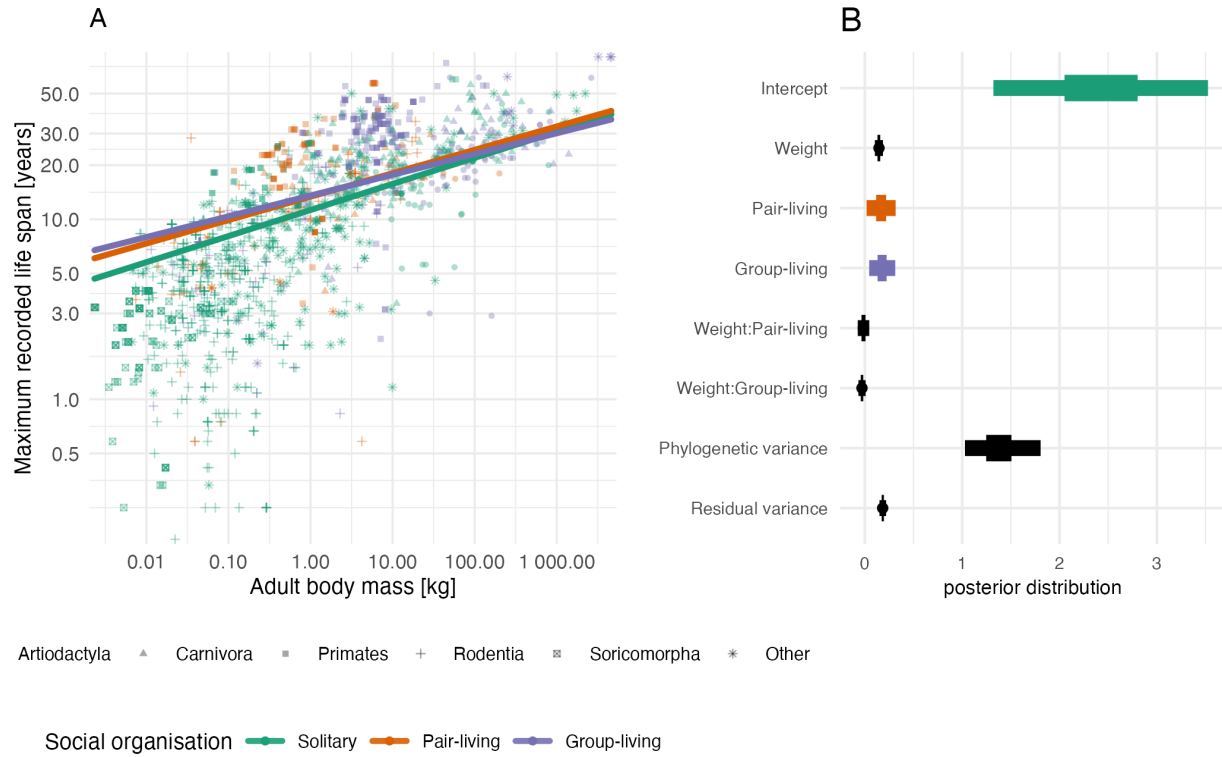


Figure 2. Interaction model ($mrls \sim wt * socialOrg$) for 1,436 mammal species. Panel A uses the same data display as Figure 1 (log-log axes, colour by social organisation, shape by order) but prediction lines come from the interaction model, allowing social categories to differ in slope as well as intercept. Panel B presents posterior summaries for all fixed effects and variance terms (point = mode; thick and thin horizontal bars = 50% and 95% credible intervals, respectively).

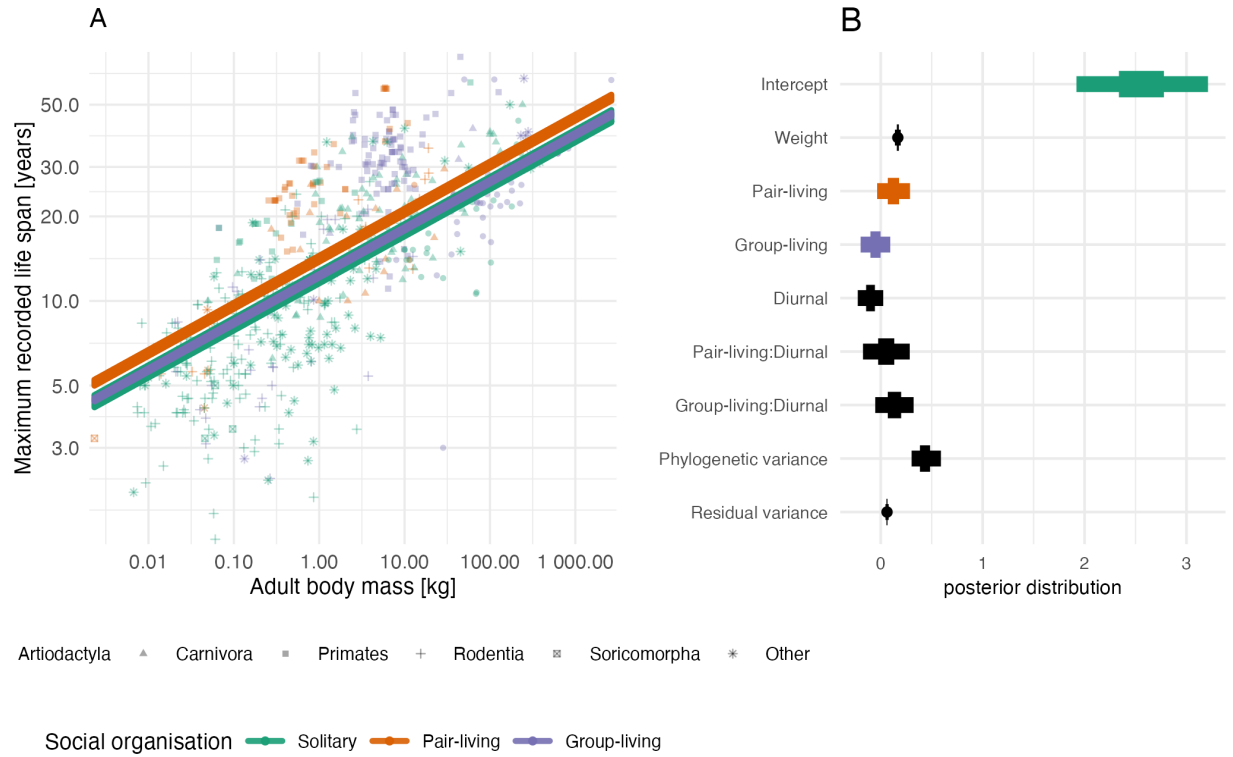


Figure 3. Activity-period interaction model ($mrls \sim wt + socialOrg * activityPeriod$) for the diurnal/nocturnal subset ($n = 611$). Panel A plots observed species values (log-log axes), with colour for social organisation and shape for order; fitted lines are model predictions across the full observed body-mass range for each social organisation and activity-period combination. Panel B gives posterior summaries for fixed effects and variance terms (point = mode; thick bar = 50% credible interval; thin bar = 95% credible interval).

Tables

Table 1. Candidate model specifications used in the analysis (n = 16 models). Models were fitted with mulTree using 25 phylogenetic trees and 4 chains per tree.

Model	Data	Formula
001	dat	mrls ~ wt + socialOrg
002	dat	mrls ~ wt * socialOrg
003	jointDat (all activity levels)	mrls ~ wt + socialOrg * activityPeriod
004	jointDat (all activity levels)	mrls ~ wt + socialOrg + activityPeriod
005	jointDat_NandD (nocturnal/diurnal)	mrls ~ wt + socialOrg * activityPeriod
006	jointDat_NandD (nocturnal/diurnal)	mrls ~ wt + socialOrg + activityPeriod
007	jointDat_NandD (nocturnal/diurnal)	mrls ~ wt + activityPeriod
008	jointDat_NandD (nocturnal/diurnal)	mrls ~ wt * activityPeriod
009	dat	mrls ~ wt + wt2 + socialOrg
010	dat	mrls ~ wt + wt2 * socialOrg
011	jointDat (all activity levels)	mrls ~ wt + wt2 + socialOrg * activityPeriod
012	jointDat (all activity levels)	mrls ~ wt + wt2 + socialOrg + activityPeriod
013	jointDat_NandD (nocturnal/diurnal)	mrls ~ wt + wt2 + socialOrg * activityPeriod
014	jointDat_NandD (nocturnal/diurnal)	mrls ~ wt + wt2 + socialOrg + activityPeriod
015	jointDat_NandD (nocturnal/diurnal)	mrls ~ wt + wt2 + activityPeriod
016	jointDat_NandD (nocturnal/diurnal)	mrls ~ wt + wt2 * activityPeriod

Table 2. Additive model (*lifespanSociality_model_001*): log maximum recorded lifespan (*mrls*) as a function of log adult body mass (*wt*; kg scale) and social organisation ($n = 1,436$). Estimates are posterior modes; intervals are 95% credible intervals (2.5% and 97.5% quantiles).

Coefficient	Estimate	Lower 95% CI	Upper 95% CI
(Intercept)	2.432	1.312	3.541
wt	0.134	0.094	0.173
socialOrgB.PairLiving	0.163	0.015	0.315
socialOrgC.GroupLiving	0.141	0.018	0.266
phylogenetic.variance	1.383	1.046	1.826
residual.variance	0.184	0.149	0.217

Table 3. Interaction model (*lifespanSociality_model_002*): log maximum recorded lifespan (*mrls*) as a function of *wt*, social organisation, and *wt:socialOrg* interaction terms ($n = 1,436$). Estimates are posterior modes with 95% credible intervals.

Coefficient	Estimate	Lower 95% CI	Upper 95% CI
(Intercept)	2.422	1.320	3.525
<i>wt</i>	0.145	0.103	0.186
<i>socialOrgB.PairLiving</i>	0.171	0.018	0.316
<i>socialOrgC.GroupLiving</i>	0.185	0.044	0.312
<i>wt:socialOrgB.PairLiving</i>	-0.015	-0.073	0.045
<i>wt:socialOrgC.GroupLiving</i>	-0.030	-0.066	0.007
<i>phylogenetic.variance</i>	1.363	1.028	1.806
<i>residual.variance</i>	0.183	0.150	0.218

Table 4. Activity-period interaction model (*lifespanSociality_model_005*): log maximum recorded lifespan (*mrls*) as a function of *wt*, social organisation, activity period (diurnal/ nocturnal subset), and *socialOrg:activityPeriod* interactions ($n = 611$). Estimates are posterior modes with 95% credible intervals.

Coefficient	Estimate	Lower 95% CI	Upper 95% CI
(Intercept)	2.547	1.920	3.211
<i>wt</i>	0.168	0.139	0.196
<i>socialOrgB.PairLiving</i>	0.126	-0.035	0.287
<i>socialOrgC.GroupLiving</i>	-0.053	-0.197	0.093
<i>activityPeriodDiurnal</i>	-0.101	-0.226	0.024
<i>socialOrgB.PairLiving:activityPeriodDiurnal</i>	0.051	-0.174	0.284
<i>socialOrgC.GroupLiving:activityPeriodDiurnal</i>	0.130	-0.054	0.322
<i>phylogenetic.variance</i>	0.436	0.303	0.590
<i>residual.variance</i>	0.061	0.046	0.078

Supporting Information

The supplementary tables below document the full model set and diagnostics. In addition to the focal models shown in the main text, we provide complete candidate-model specifications and posterior summaries for all fitted models (*lifespanSociality_model_001* to *lifespanSociality_model_016*).

Table S1. Posterior summaries for the quadratic additive model (*lifespanSociality_model_009*; $mrls \sim wt + wt^2 + socialOrg$; $n = 1,436$). Estimates are posterior modes with 95% credible intervals. Coefficients whose intervals exclude zero have strongest support for directional effects on log maximum lifespan.

Coefficient	Estimate	Lower 95% CI	Upper 95% CI
(Intercept)	2.427	1.309	3.517
wt	0.133	0.093	0.173
wt ²	0.001	-0.006	0.008
socialOrgB.PairLiving	0.166	0.014	0.315
socialOrgC.GroupLiving	0.140	0.014	0.264
phylogenetic.variance	1.378	1.045	1.815
residual.variance	0.183	0.150	0.217

Table S2. Posterior summaries for the quadratic interaction model (*lifespanSociality_model_010*; $mrls \sim wt + wt^2$ * *socialOrg*; $n = 1,436$). Estimates are posterior modes with 95% credible intervals. Interaction terms test whether linear and quadratic body-mass effects differ among social-organisation categories.

Coefficient	Estimate	Lower 95% CI	Upper 95% CI
(Intercept)	2.438	1.292	3.525
wt	0.134	0.093	0.175
wt2	0.002	-0.006	0.010
socialOrgB.PairLiving	0.185	-0.005	0.384
socialOrgC.GroupLiving	0.165	0.000	0.333
wt2:socialOrgB.PairLiving	-0.004	-0.023	0.016
wt2:socialOrgC.GroupLiving	-0.003	-0.012	0.007
phylogenetic.variance	1.394	1.055	1.809
residual.variance	0.183	0.150	0.217

Table S3. Complete candidate model inventory. For each model, we report the model identifier, output file prefix, analysis dataset, number of species, and fixed-effects formula. This table defines the full model set used for primary and sensitivity analyses.

Model	Model file	Dataset	Species (n)	Formula
001	lifespanSociality_model_001	dat	1,436	mrls ~ wt + socialOrg
002	lifespanSociality_model_002	dat	1,436	mrls ~ wt * socialOrg
003	lifespanSociality_model_003	jointDat (all activity levels)	804	mrls ~ wt + socialOrg * activityPeriod
004	lifespanSociality_model_004	jointDat (all activity levels)	804	mrls ~ wt + socialOrg + activityPeriod
005	lifespanSociality_model_005	jointDat_NandD (nocturnal/diurnal)	611	mrls ~ wt + socialOrg * activityPeriod
006	lifespanSociality_model_006	jointDat_NandD (nocturnal/diurnal)	611	mrls ~ wt + socialOrg + activityPeriod
007	lifespanSociality_model_007	jointDat_NandD (nocturnal/diurnal)	611	mrls ~ wt + activityPeriod
008	lifespanSociality_model_008	jointDat_NandD (nocturnal/diurnal)	611	mrls ~ wt * activityPeriod
009	lifespanSociality_model_009	dat	1,436	mrls ~ wt + wt2 + socialOrg
010	lifespanSociality_model_010	dat	1,436	mrls ~ wt + wt2 * socialOrg
011	lifespanSociality_model_011	jointDat (all activity levels)	804	mrls ~ wt + wt2 + socialOrg * activityPeriod
012	lifespanSociality_model_012	jointDat (all activity levels)	804	mrls ~ wt + wt2 + socialOrg + activityPeriod
013	lifespanSociality_model_013	jointDat_NandD (nocturnal/diurnal)	611	mrls ~ wt + wt2 + socialOrg * activityPeriod
014	lifespanSociality_model_014	jointDat_NandD (nocturnal/diurnal)	611	mrls ~ wt + wt2 + socialOrg + activityPeriod
015	lifespanSociality_model_015	jointDat_NandD (nocturnal/diurnal)	611	mrls ~ wt + wt2 + activityPeriod
016	lifespanSociality_model_016	jointDat_NandD (nocturnal/diurnal)	611	mrls ~ wt + wt2 * activityPeriod

Table S4. Posterior summaries for all coefficients across the full candidate model set (models 001-016). Estimates are posterior modes with 95% credible intervals. Term type distinguishes fixed effects from variance components, enabling comparison of parameter support across models.

Model	Model file	Term type	Coefficient	Estimate	Lower 95% CI	Upper 95% CI
001	lifespanSociality_model_001	fixed	(Intercept)	2.432	1.312	3.541
001	lifespanSociality_model_001	fixed	wt	0.134	0.094	0.173
001	lifespanSociality_model_001	fixed	socialOrgB.PairLiving	0.163	0.015	0.315
001	lifespanSociality_model_001	fixed	socialOrgC.GroupLiving	0.141	0.018	0.266
001	lifespanSociality_model_001	variance	phylogenetic.variance	1.383	1.046	1.826
001	lifespanSociality_model_001	variance	residual.variance	0.184	0.149	0.217
002	lifespanSociality_model_002	fixed	(Intercept)	2.422	1.320	3.525
002	lifespanSociality_model_002	fixed	wt	0.145	0.103	0.186
002	lifespanSociality_model_002	fixed	socialOrgB.PairLiving	0.171	0.018	0.316
002	lifespanSociality_model_002	fixed	socialOrgC.GroupLiving	0.185	0.044	0.312
002	lifespanSociality_model_002	fixed	wt:socialOrgB.PairLiving	-0.015	-0.073	0.045
002	lifespanSociality_model_002	fixed	wt:socialOrgC.GroupLiving	-0.030	-0.066	0.007
002	lifespanSociality_model_002	variance	phylogenetic.variance	1.363	1.028	1.806
002	lifespanSociality_model_002	variance	residual.variance	0.183	0.150	0.218
003	lifespanSociality_model_003	fixed	(Intercept)	2.490	1.873	3.104
003	lifespanSociality_model_003	fixed	wt	0.161	0.136	0.186
003	lifespanSociality_model_003	fixed	socialOrgB.PairLiving	0.202	0.024	0.378
003	lifespanSociality_model_003	fixed	socialOrgC.GroupLiving	0.110	-0.019	0.240
003	lifespanSociality_model_003	fixed	activityPeriodB.nocturnal	0.119	-0.003	0.237
003	lifespanSociality_model_003	fixed	activityPeriodC.cathemeral	0.070	-0.062	0.204
003	lifespanSociality_model_003	fixed	activityPeriodD.crepuscular	0.107	-0.080	0.274
003	lifespanSociality_model_003	fixed	socialOrgB.PairLiving:activityPeriodB.nocturnal	-0.051	-0.275	0.180
003	lifespanSociality_model_003	fixed	socialOrgC.GroupLiving:activityPeriodB.nocturnal	-0.138	-0.333	0.044
003	lifespanSociality_model_003	fixed	socialOrgB.PairLiving:activityPeriodC.cathemeral	0.053	-0.192	0.302
003	lifespanSociality_model_003	fixed	socialOrgC.GroupLiving:activityPeriodC.cathemeral	-0.010	-0.208	0.185
003	lifespanSociality_model_003	fixed	socialOrgB.PairLiving:activityPeriodD.crepuscular	-0.060	-0.468	0.331
003	lifespanSociality_model_003	fixed	socialOrgC.GroupLiving:activityPeriodD.crepuscular	-0.153	-0.435	0.123
003	lifespanSociality_model_003	variance	phylogenetic.variance	0.404	0.287	0.545
003	lifespanSociality_model_003	variance	residual.variance	0.068	0.053	0.083
004	lifespanSociality_model_004	fixed	(Intercept)	2.524	1.918	3.141
004	lifespanSociality_model_004	fixed	wt	0.160	0.135	0.186
004	lifespanSociality_model_004	fixed	socialOrgB.PairLiving	0.187	0.075	0.289
004	lifespanSociality_model_004	fixed	socialOrgC.GroupLiving	0.051	-0.035	0.136

Model	Model file	Term type	Coefficient	Estimate	Lower 95% CI	Upper 95% CI
004	lifespanSociality_model_004	fixed	activityPeriodB.nocturnal	0.073	-0.023	0.169
004	lifespanSociality_model_004	fixed	activityPeriodC.cathemeral	0.066	-0.035	0.165
004	lifespanSociality_model_004	fixed	activityPeriodD.crepuscular	0.036	-0.097	0.169
004	lifespanSociality_model_004	variance	phylogenetic.variance	0.409	0.294	0.548
004	lifespanSociality_model_004	variance	residual.variance	0.066	0.053	0.082
005	lifespanSociality_model_005	fixed	(Intercept)	2.547	1.920	3.211
005	lifespanSociality_model_005	fixed	wt	0.168	0.139	0.196
005	lifespanSociality_model_005	fixed	socialOrgB.PairLiving	0.126	-0.035	0.287
005	lifespanSociality_model_005	fixed	socialOrgC.GroupLiving	-0.053	-0.197	0.093
005	lifespanSociality_model_005	fixed	activityPeriodDiurnal	-0.101	-0.226	0.024
005	lifespanSociality_model_005	fixed	socialOrgB.PairLiving:activityPeriodDiurnal	0.051	-0.174	0.284
005	lifespanSociality_model_005	fixed	socialOrgC.GroupLiving:activityPeriodDiurnal	0.130	-0.054	0.322
005	lifespanSociality_model_005	variance	phylogenetic.variance	0.436	0.303	0.590
005	lifespanSociality_model_005	variance	residual.variance	0.061	0.046	0.078
006	lifespanSociality_model_006	fixed	(Intercept)	2.540	1.905	3.220
006	lifespanSociality_model_006	fixed	wt	0.168	0.139	0.196
006	lifespanSociality_model_006	fixed	socialOrgB.PairLiving	0.138	0.014	0.260
006	lifespanSociality_model_006	fixed	socialOrgC.GroupLiving	0.021	-0.079	0.119
006	lifespanSociality_model_006	fixed	activityPeriodDiurnal	-0.057	-0.162	0.046
006	lifespanSociality_model_006	variance	phylogenetic.variance	0.443	0.306	0.607
006	lifespanSociality_model_006	variance	residual.variance	0.060	0.045	0.077
007	lifespanSociality_model_007	fixed	(Intercept)	2.561	1.902	3.232
007	lifespanSociality_model_007	fixed	wt	0.165	0.138	0.195
007	lifespanSociality_model_007	fixed	activityPeriodDiurnal	-0.053	-0.155	0.052
007	lifespanSociality_model_007	variance	phylogenetic.variance	0.453	0.324	0.616
007	lifespanSociality_model_007	variance	residual.variance	0.059	0.044	0.076
008	lifespanSociality_model_008	fixed	(Intercept)	2.573	1.911	3.231
008	lifespanSociality_model_008	fixed	wt	0.162	0.130	0.192
008	lifespanSociality_model_008	fixed	activityPeriodDiurnal	-0.065	-0.173	0.041
008	lifespanSociality_model_008	fixed	wt:activityPeriodDiurnal	0.018	-0.017	0.051
008	lifespanSociality_model_008	variance	phylogenetic.variance	0.456	0.318	0.618
008	lifespanSociality_model_008	variance	residual.variance	0.059	0.044	0.076
009	lifespanSociality_model_009	fixed	(Intercept)	2.427	1.309	3.517
009	lifespanSociality_model_009	fixed	wt	0.133	0.093	0.173
009	lifespanSociality_model_009	fixed	wt2	0.001	-0.006	0.008
009	lifespanSociality_model_009	fixed	socialOrgB.PairLiving	0.166	0.014	0.315

Model	Model file	Term type	Coefficient	Estimate	Lower 95% CI	Upper 95% CI
009	lifespanSociality_model_009	fixed	socialOrgC.GroupLiving	0.140	0.014	0.264
009	lifespanSociality_model_009	variance	phylogenetic.variance	1.378	1.045	1.815
009	lifespanSociality_model_009	variance	residual.variance	0.183	0.150	0.217
010	lifespanSociality_model_010	fixed	(Intercept)	2.438	1.292	3.525
010	lifespanSociality_model_010	fixed	wt	0.134	0.093	0.175
010	lifespanSociality_model_010	fixed	wt2	0.002	-0.006	0.010
010	lifespanSociality_model_010	fixed	socialOrgB.PairLiving	0.185	-0.005	0.384
010	lifespanSociality_model_010	fixed	socialOrgC.GroupLiving	0.165	0.000	0.333
010	lifespanSociality_model_010	fixed	wt2:socialOrgB.PairLiving	-0.004	-0.023	0.016
010	lifespanSociality_model_010	fixed	wt2:socialOrgC.GroupLiving	-0.003	-0.012	0.007
010	lifespanSociality_model_010	variance	phylogenetic.variance	1.394	1.055	1.809
010	lifespanSociality_model_010	variance	residual.variance	0.183	0.150	0.217
011	lifespanSociality_model_011	fixed	(Intercept)	2.481	1.871	3.097
011	lifespanSociality_model_011	fixed	wt	0.160	0.134	0.186
011	lifespanSociality_model_011	fixed	wt2	0.001	-0.004	0.006
011	lifespanSociality_model_011	fixed	socialOrgB.PairLiving	0.202	0.025	0.380
011	lifespanSociality_model_011	fixed	socialOrgC.GroupLiving	0.108	-0.021	0.240
011	lifespanSociality_model_011	fixed	activityPeriodB.nocturnal	0.121	-0.002	0.237
011	lifespanSociality_model_011	fixed	activityPeriodC.cathemeral	0.072	-0.060	0.205
011	lifespanSociality_model_011	fixed	activityPeriodD.crepuscular	0.097	-0.082	0.272
011	lifespanSociality_model_011	fixed	socialOrgB.PairLiving:activityPeriodB.nocturnal	-0.046	-0.277	0.180
011	lifespanSociality_model_011	fixed	socialOrgC.GroupLiving:activityPeriodB.nocturnal	-0.138	-0.333	0.044
011	lifespanSociality_model_011	fixed	socialOrgB.PairLiving:activityPeriodC.cathemeral	0.051	-0.199	0.303
011	lifespanSociality_model_011	fixed	socialOrgC.GroupLiving:activityPeriodC.cathemeral	-0.015	-0.210	0.187
011	lifespanSociality_model_011	fixed	socialOrgB.PairLiving:activityPeriodD.crepuscular	-0.063	-0.474	0.336
011	lifespanSociality_model_011	fixed	socialOrgC.GroupLiving:activityPeriodD.crepuscular	-0.150	-0.440	0.120
011	lifespanSociality_model_011	variance	phylogenetic.variance	0.405	0.291	0.543
011	lifespanSociality_model_011	variance	residual.variance	0.068	0.054	0.083
012	lifespanSociality_model_012	fixed	(Intercept)	2.513	1.914	3.128
012	lifespanSociality_model_012	fixed	wt	0.159	0.133	0.186
012	lifespanSociality_model_012	fixed	wt2	0.001	-0.004	0.006
012	lifespanSociality_model_012	fixed	socialOrgB.PairLiving	0.174	0.074	0.288
012	lifespanSociality_model_012	fixed	socialOrgC.GroupLiving	0.049	-0.037	0.135
012	lifespanSociality_model_012	fixed	activityPeriodB.nocturnal	0.072	-0.023	0.168
012	lifespanSociality_model_012	fixed	activityPeriodC.cathemeral	0.061	-0.034	0.166
012	lifespanSociality_model_012	fixed	activityPeriodD.crepuscular	0.031	-0.098	0.168

Model	Model file	Term type	Coefficient	Estimate	Lower 95% CI	Upper 95% CI
012	lifespanSociality_model_012	variance	phylogenetic.variance	0.403	0.294	0.550
012	lifespanSociality_model_012	variance	residual.variance	0.066	0.053	0.082
013	lifespanSociality_model_013	fixed	(Intercept)	2.566	1.909	3.213
013	lifespanSociality_model_013	fixed	wt	0.166	0.138	0.196
013	lifespanSociality_model_013	fixed	wt2	0.000	-0.005	0.007
013	lifespanSociality_model_013	fixed	socialOrgB.PairLiving	0.125	-0.037	0.286
013	lifespanSociality_model_013	fixed	socialOrgC.GroupLiving	-0.056	-0.201	0.091
013	lifespanSociality_model_013	fixed	activityPeriodDiurnal	-0.104	-0.228	0.023
013	lifespanSociality_model_013	fixed	socialOrgB.PairLiving:activityPeriodDiurnal	0.058	-0.174	0.286
013	lifespanSociality_model_013	fixed	socialOrgC.GroupLiving:activityPeriodDiurnal	0.140	-0.055	0.326
013	lifespanSociality_model_013	variance	phylogenetic.variance	0.434	0.298	0.594
013	lifespanSociality_model_013	variance	residual.variance	0.061	0.046	0.078
014	lifespanSociality_model_014	fixed	(Intercept)	2.552	1.899	3.213
014	lifespanSociality_model_014	fixed	wt	0.168	0.138	0.196
014	lifespanSociality_model_014	fixed	wt2	0.000	-0.006	0.006
014	lifespanSociality_model_014	fixed	socialOrgB.PairLiving	0.138	0.013	0.260
014	lifespanSociality_model_014	fixed	socialOrgC.GroupLiving	0.020	-0.080	0.119
014	lifespanSociality_model_014	fixed	activityPeriodDiurnal	-0.057	-0.162	0.048
014	lifespanSociality_model_014	variance	phylogenetic.variance	0.445	0.310	0.607
014	lifespanSociality_model_014	variance	residual.variance	0.059	0.045	0.077
015	lifespanSociality_model_015	fixed	(Intercept)	2.582	1.901	3.230
015	lifespanSociality_model_015	fixed	wt	0.166	0.137	0.195
015	lifespanSociality_model_015	fixed	wt2	0.001	-0.006	0.006
015	lifespanSociality_model_015	fixed	activityPeriodDiurnal	-0.052	-0.157	0.052
015	lifespanSociality_model_015	variance	phylogenetic.variance	0.458	0.324	0.622
015	lifespanSociality_model_015	variance	residual.variance	0.059	0.044	0.075
016	lifespanSociality_model_016	fixed	(Intercept)	2.562	1.879	3.230
016	lifespanSociality_model_016	fixed	wt	0.169	0.139	0.198
016	lifespanSociality_model_016	fixed	wt2	0.002	-0.005	0.009
016	lifespanSociality_model_016	fixed	activityPeriodDiurnal	-0.005	-0.139	0.125
016	lifespanSociality_model_016	fixed	wt2:activityPeriodDiurnal	-0.005	-0.015	0.005
016	lifespanSociality_model_016	variance	phylogenetic.variance	0.458	0.328	0.628
016	lifespanSociality_model_016	variance	residual.variance	0.058	0.044	0.075

Table S5. Gelman-Rubin convergence diagnostics (PSRF) by model across tree-level fits. Reported values include median and maximum multivariate PSRF (mPSRF), and median and worst per-parameter PSRF. Values near 1 indicate good between-chain convergence; persistent values above approximately 1.1 indicate potential convergence concerns.

model	trees	median_mpsrf	max_mpsrf	median_max_psr	worst_max_psr	total_params_over_1_1
001	25	1.014	1.087	1.016	1.077	0
002	25	1.015	1.064	1.021	1.062	0
003	25	1.024	1.072	1.024	1.062	0
004	25	1.034	1.143	1.036	1.136	1
005	25	1.025	1.100	1.025	1.104	1
006	25	1.033	1.101	1.036	1.096	0
007	25	1.031	1.109	1.029	1.100	1
008	25	1.029	1.086	1.027	1.091	0
009	25	1.013	1.088	1.012	1.081	0
010	25	1.020	1.065	1.019	1.058	0
011	25	1.034	1.124	1.034	1.122	1
012	25	1.026	1.125	1.025	1.121	1
013	25	1.031	1.110	1.036	1.112	2
014	25	1.034	1.166	1.029	1.154	2
015	25	1.023	1.092	1.025	1.085	0
016	25	1.038	1.129	1.037	1.122	3

Table S6. Effective sample size (ESS) diagnostics by model across all chain files. ESS summaries are based on each chain's minimum ESS across fixed and variance parameters (worst-sampled parameter per chain). Higher ESS indicates greater Monte Carlo precision; counts below 200 and 500 provide conservative flags for potentially under-sampled chains.

model	chain_files	min_chain_ess	median_chain_ess	p10_chain_ess	chains_below_200	chains_below_500
001	100	38.5	73.7	56.2	100	100
002	100	41.9	74.1	55.6	100	100
003	100	25.8	45.5	35.9	100	100
004	100	26.0	48.2	36.4	100	100
005	100	21.7	38.8	30.5	100	100
006	100	17.8	40.0	31.5	100	100
007	100	29.8	43.5	34.9	100	100
008	100	22.6	41.4	31.8	100	100
009	100	45.5	76.5	60.1	100	100
010	100	44.0	75.8	59.5	100	100
011	100	22.9	46.4	35.2	100	100
012	100	21.2	45.8	33.9	100	100
013	100	20.2	38.2	29.8	100	100
014	100	24.6	41.7	32.1	100	100
015	100	24.8	42.0	31.4	100	100
016	100	24.2	42.9	33.8	100	100

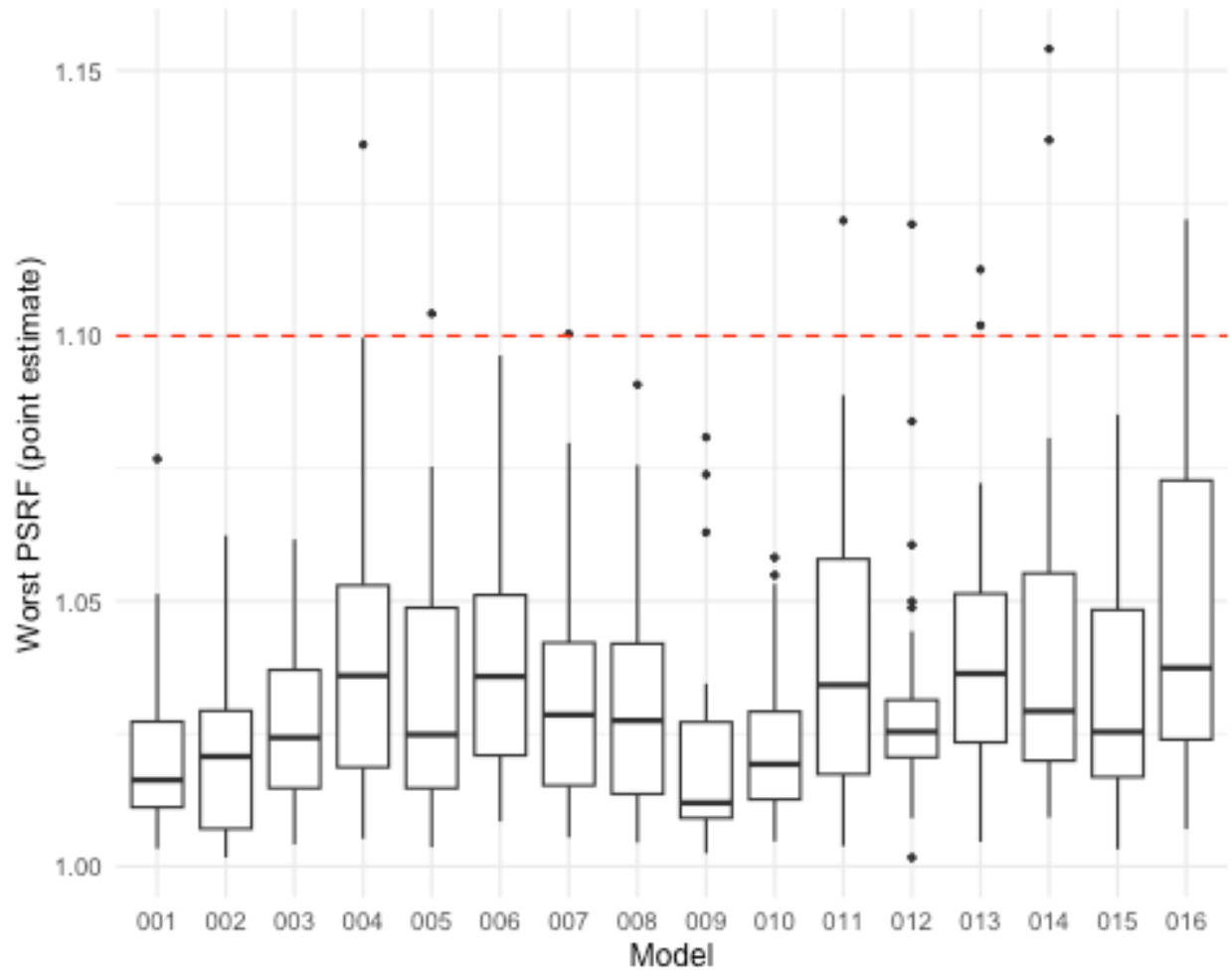


Figure S1. Distribution of worst per-parameter Gelman-Rubin potential scale reduction factors (PSRF) across phylogenetic trees for each model. For each tree-level fit, the plotted value is the largest PSRF among monitored parameters, so higher values indicate poorer between-chain mixing for at least one parameter. Values close to 1 indicate convergence; the dashed line at 1.1 marks a commonly used threshold above which convergence may be inadequate.