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14 **Most modern mammals, including strictly diurnal species, exhibit sensory adaptations**
15 **to nocturnal activity, thought to be the result of a prolonged nocturnal phase or**
16 **'bottleneck' during early mammalian evolution. Nocturnality may have allowed**
17 **mammals to avoid antagonistic interactions with diurnal dinosaurs during the**
18 **Mesozoic. However, understanding the evolution of mammalian activity patterns is**
19 **hindered by scant and ambiguous fossil evidence. While ancestral reconstructions of**
20 **behavioural traits from extant species have the potential to elucidate these patterns,**
21 **existing studies have been limited in taxonomic scope. Here, we use an extensive**
22 **behavioural dataset for 2415 species from all extant orders to reconstruct ancestral**
23 **activity patterns across Mammalia. We find strong support for the nocturnal origin of**
24 **mammals and the Cenozoic appearance of diurnality, although cathemerality (mixed**
25 **diel periodicity) may have appeared in the late Cretaceous. Simian primates are among**
26 **the earliest mammals to exhibit strict diurnal activity, some 52-33Mya. Our study is**
27 **consistent with the hypothesis that temporal partitioning between early mammals and**
28 **dinosaurs during the Mesozoic led to a mammalian nocturnal bottleneck, but also**
29 **demonstrates the need for improved phylogenetic estimates for Mammalia.**

30 Although mammals exhibit striking morphological, behavioural and ecological niche
31 diversity¹, the distribution of mammalian activity patterns is strongly biased towards
32 nocturnality². Additionally, most mammalian species, including strictly diurnal ones, exhibit
33 visual adaptations to nocturnal activity that are similar to those of nocturnal birds and
34 reptiles³. For example, mammals lack photoreception mechanisms (e.g. parietal organs) that
35 are found in other amniotes³, and exhibit reduced diversity of active photoreceptors^{4,5}.
36 Additionally, there is evidence that enhanced olfactory sensitivity⁶, broader frequency range
37 hearing⁷, and sophisticated whisker-mediated tactile perception⁸ may have evolved in
38 mammals to compensate for insufficient visual information^{3,5}. In general, species exhibit

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39 characteristic patterns of activity distribution over the 24-hour (diel) cycle, and as
40 environmental conditions may change radically, yet predictably between day and night,
41 activity patterns allow individuals to anticipate fluctuations, and time activity optimally^{9,10}.
42 Physiological and behavioural adaptations to different activity patterns are significant to
43 individual fitness¹¹, and therefore to species evolutionary success^{12,13}. Moreover, long-term
44 shifts in activity patterns may reveal shifts in selective regimes, caused by changes in biotic
45 and abiotic conditions^{13,14}.

46 The predominance of nocturnal adaptations in mammals may be the result of a
47 prolonged nocturnal phase in the early stages of mammalian evolution, after which emerged
48 the more diverse patterns observed today^{5,15}. This ‘nocturnal bottleneck’ hypothesis suggests
49 that mammals were restricted to nocturnal activity by antagonistic interactions with the
50 ecologically dominant diurnal dinosaurs during the Mesozoic^{5,15,16}. The Cretaceous-
51 Paleogene (K-Pg) mass extinction event circa 66Mya, led to the extinction of all non-avian
52 dinosaurs along with the marine- and flying reptiles, and the majority of other vertebrates,
53 and invertebrate and plant taxa^{17,18}. This event marks the end of the Mesozoic ‘reign of
54 dinosaurs’ and the transition to the mammal-dominated Cenozoic fauna. If an antagonistic
55 interaction with dinosaurs was an important factor in restricting early mammals to nocturnal
56 activity, then all Mesozoic mammals are expected to have been nocturnal, and diurnal
57 mammals would have only appeared after the K-Pg mass extinction event.

58 Support for the nocturnal bottleneck hypothesis remains indirect. For example, some
59 Synapsids, the non-mammalian lineage ancestral to mammals, were adapted to nocturnal
60 activity >300Mya, suggesting a nocturnal origin for mammals¹⁹. However, as all modern
61 mammals (except monkeys and apes) have nocturnal morphological adaptations regardless of
62 their activity^{3,20}, inferring activity patterns from fossil cranial morphology may be unreliable.
63 Evidence from genetic and histological studies of the evolutionary development of

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64 mammalian eyes indicate that nocturnal adaptations preceded diurnal ones^{4,21}, but this does
65 not help elucidate questions around the timing of these adaptations. Ancestral reconstructions
66 of behavioural traits using a phylogenetic comparative approach may help to understand both
67 the pattern and timing of the evolution of activity patterns in mammals since activity patterns
68 have been shown to be genetically determined²² yet responsive to selective pressures¹⁰.
69 However, phylogenetic studies of mammalian activity patterns so far have focused on two
70 mammalian orders – primates²³⁻²⁵ and rodents²⁶. Primate activity patterns have been studied
71 extensively, and some evidence suggests that primate diurnality originated in the most recent
72 common ancestor (MRCA) of suborder Haplorrhini (all monkeys, apes and tarsiers)¹³ in the
73 Mesozoic^{27,28}. It is conceivable, although thus far not tested, that diurnal diversifications in
74 other orders of Mesozoic origins, e.g. Scandentia (treeshrews), Macroscelidea (elephant
75 shrews) and Rodentia, could have occurred before the extinction of dinosaurs, calling for a
76 wider examination of how activity patterns evolved across mammals.

77 Here, we use an extensive dataset of activity patterns for 2415 mammal species,
78 representing 135 of the 148 extant families and all extant orders (Supplementary Table 1) to
79 investigate ancestral activity patterns in mammals, and to understand the timings of the
80 appearance of mammal diurnality. We assign species to one of five activity patterns: (i)
81 nocturnal – active only or mostly in the dark; (ii) diurnal – active only or mostly during
82 daylight hours; (iii) cathemeral – active both during the day and during the night; (iv)
83 crepuscular – active only at twilight, around sunrise and/or sunset; and (v) ultradian – active
84 in cycles of a few hours. (see Methods). We map the three main activity patterns (nocturnal,
85 cathemeral, and diurnal) onto two phylogenetic frameworks representing two of the main
86 hypotheses of mammalian evolutionary history for our analyses, termed here short-fuse (SF)
87 following²⁸ updated by²⁹, and long-fuse (LF) phylogenies (adapted from²⁷) (Fig. 1). We then
88 use reversible jump Markov Chain Monte Carlo (rjMCMC) methods³⁰ to estimate transition

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89 rates between different activity states, and to infer the posterior probability (PP) of character
90 states at each node in the phylogenies to examine the evolution of activity patterns of
91 mammals and estimate support for the nocturnal bottleneck hypothesis.

92 **Results**

93 We find that the model values of PP_{Noct} (posterior probability of nocturnality) at the ancestral
94 node of extant mammals were 0.74 (Credible Interval, CI 0.71-0.76) and 0.59 (CI 0.54-0.64)
95 for SF and LF phylogenies, respectively, offering strong support for a nocturnal ancestor (Fig.
96 2). In contrast, a cathemeral or a diurnal ancestral state is less well supported: modal value of
97 PP_{Cath} (posterior probability of cathemerality) = 0.24 (CI 0.23-0.26) and 0.31 (CI 0.29-0.33)
98 for SF and LF, respectively, or PP_{Diur} (posterior probability of diurnality) = 0.02 (CI 0.01-
99 0.03) SF and 0.1 (CI 0.07-0.14) LF (Fig. 2). The narrow and non-overlapping distributions of
100 PP values across the activity pattern reconstructions indicate that our results are consistent
101 and robust across samples of the rjMCMC chains, although the distributions are wider using
102 the LF phylogeny (Fig. 2).

103 The first strong evidence (where the reconstructed activity pattern was supported by
104 modal PP values >0.67) in mammals of an expansion of temporal niche into cathemerality, is
105 in the early Paleogene (Cenozoic) for the SF phylogeny (no later than 65.8Mya), or in the late
106 Cretaceous (Mesozoic) for the LF phylogeny (no later than 74.7Mya) (Figs. 3 and 4).
107 Although the LF phylogeny supports a Mesozoic shift to cathemerality, the modal PP values
108 of the remaining 41 Mesozoic nodes were either nocturnal (23 nodes), or unclear – where all
109 three activity patterns were supported by modal PP values <0.67 (18 nodes). Using the SF
110 phylogeny, we reconstruct the first transition to cathemerality in the MRCA of order
111 Cetartiodactyla (cetaceans and even-toed ungulates). This taxa was likely to be cathemeral
112 ($PP_{\text{Cath}} = 0.79$ CI 0.72-0.87), and almost certainly exhibited considerable daytime activity

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113 (PP_{Noct} = 0.02 CI 0.01-0.04) (Fig. 3). Using the LF phylogeny, the first cathemeral transition
114 was in the MRCA of families Soricidae (shrews) and Talpidae (moles) (PP_{Cath} = 0.81 CI
115 0.61-0.91; PP_{Diur} = 0.07 CI 0.03-0.15) (Fig. 4).

116 Evidence of the evolution of diurnality (modal PP values >0.67) first appears in the
117 early Paleogene (no later than 52.4Mya or 63.8Mya for SF and LF phylogeny, respectively)
118 (Figs. 3 and 4). Using the SF phylogeny, we reconstruct transition to diurnality in the MRCA
119 of the Simiiformes (all monkeys and apes) (PP_{Diur} = 0.76, CI 0.75-0.78; PP_{Cath} = 0.23, CI
120 0.22-0.25) (Fig.3). Using the LF phylogeny, the first taxon to exhibit diurnal activity was the
121 MRCA of the family Macroscelididae (elephant shrews) (PP_{Diur} = 0.77, CI 0.76-0.80; PP_{Cath} =
122 0.22, CI 0.19-0.23; 63.8Mya), followed by the MRCA of families Ctenodactylidae (comb
123 rats, Rodentia) (PP_{Diur} = 0.76; CI 0.73-0.78; 61.6Mya), Camelidae (Cetartiodactyla) (PP_{Diur} =
124 0.74, CI 0.72-0.77; 59.6Mya), and Tupaiidae (treeshrews, Scandentia) (PP_{Diur} = 0.99, CI
125 0.99-0.99; 51.1Mya) in rapid succession (Fig. 4).

126 For both SF and LF phylogenies, we find that transition rates from a cathemeral pattern to
127 either nocturnal or diurnal are about three times higher than the transition rates from either
128 nocturnal or diurnal to cathemeral (Table 1). Furthermore, the transition rates in the SF
129 reconstruction are three orders of magnitude lower than the respective rates in the LF
130 reconstruction.

131 Discussion

132 We have shown that extant mammals likely originated from a nocturnal ancestor, and that
133 these ancestors remained nocturnal throughout the Mesozoic until either 9 Myr before the K-
134 Pg event (LF reconstruction), or just after it (SF reconstruction). On balance, our evidence
135 suggests that mammals likely remained nocturnal throughout the Mesozoic as nocturnal
136 activity is strongly supported at most Mesozoic nodes in both SF and LF reconstructions. We

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137 find strong evidence that the shift to strict diurnality occurred after the K-Pg event (both SF
138 and LF reconstructions), although cathemerality may have appeared in the late Cretaceous
139 (74.7Mya LF reconstruction). Combined with other sources of evidence^{5,21}, our analysis helps
140 to further establish the nocturnal ancestry of mammals and the timing of the evolution of
141 diurnality, as predicted by the nocturnal bottleneck hypothesis, namely that diurnality only
142 originated in mammals after the disappearance of the dinosaurs.

143 Even if we accept the appearance of cathemeral mammals as an expansion of the
144 temporal niche before the K-Pg event, it does not necessarily provide strong evidence against
145 the nocturnal bottleneck hypothesis. Declines in dinosaur diversity long before the K-Pg
146 event have been suggested, either globally, starting at least 40Myr before the K-Pg event³¹, or
147 locally – herbivorous dinosaurs in present-day North America were declining for up to
148 15Myr prior to the event¹⁸. In contrast, fossils show that mammals had evolved considerable
149 eco-morphological diversity as early as the mid-Jurassic period (174-164 Mya), and
150 diversified along all axes of the ecological niche^{32,33}, except the temporal axis. Moreover,
151 extensive mammal radiations occurred following the Cretaceous Terrestrial Revolution
152 (KTR, 120-80Mya), whereby angiosperms rose to dominate the global flora, and
153 revolutionised eco-space^{27,34,35}. Under such conditions, an invasion of mammals into the
154 temporal niche of declining dinosaurs does not violate the assumption of temporal
155 partitioning.

156 The MRCA of infraorder Simiiformes (monkeys and apes) was among the first taxa to
157 have evolved diurnality (52.4Mya, SF reconstruction), and this is consistent with their
158 evolution of diurnally-adapted vision^{3,4,20} – a singularity in mammals. Other diurnal clades
159 such as squirrels (Sciuridae) and elephant-shrews (Macroscelididae) evolved at about the
160 same time as the Simiiformes^{27,28} and presumably had similar opportunity to evolve
161 diurnally-adapted vision, suggesting that diurnality in Simiiformes may have evolved

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162 considerably earlier than the minimum date of 52.4Mya. Simiiformes lie on an evolutionary
163 branch that originates 83.2Mya (SF), when they diverged from tarsiers – their closest living
164 relatives in the suborder Haplorrhini. Tarsiers are strictly nocturnal, but share with the
165 Simiiformes several adaptations for high visual acuity, typical to diurnal vision^{25,36}. The
166 morphological and physiological adaptations to nocturnality in tarsiers are unlike those of any
167 other nocturnal primate, suggesting that tarsiers originated from a diurnal ancestor, the
168 MRCA of Haplorrhini, and secondarily adapted to nocturnal life¹³. The Haplorrhine MRCA
169 was a Mesozoic species that lived until 83.2Mya (SF) or 78.1Mya (LF). This would imply
170 that Mesozoic mammals were able to break out of the nocturnal bottleneck and endure direct
171 interaction with dinosaurs following the KTR. Nevertheless, both reconstructions here, as
172 well as other reconstructions of primate activity patterns based on different sets of data,
173 including data on visual physiology, find weak or no evidence to the diurnality of the
174 Haplorrhine MRCA²³⁻²⁵.

175 There are other uncertainties around the dates for three of the four taxa identified as
176 shifting to diurnality within 7Myr after the K-Pg in the LF reconstruction (Macroscelididea,
177 Ctenodactylidae, Camelidae). This is due to how we re-scaled the terminal-branches in²⁷ to
178 produce the species-level LF phylogeny. However, according to the dates given in²⁷ and
179 additional studies supporting the LF hypothesis³⁷⁻⁴⁰, these families originated in the
180 Cenozoic, so our prediction of Cenozoic origins to mammal diurnality remains intact. The
181 MRCA of Tupaiidae (Scandentia) and their closest living relative – the nocturnal
182 Ptilocercidae (Pen-tailed tree shrews, a monotypic family) – has been placed in the Cenozoic,
183 60.1 Mya²⁷ The LF reconstruction shows that this species was probably diurnal or
184 cathemeral, but neither pattern was supported by PP values >0.67.

185 On both SF and LF reconstructions, the rates of transition from cathemeral activity to
186 either nocturnal or diurnal imply that the diurnal and nocturnal niches may be more

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187 favourable for mammals. However, our results unequivocally support the persistence of
188 cathemerality in mammals since the K-Pg. In primates, cathemerality has been argued
189 adaptive under fluctuating environmental conditions^{23,41} and cathemeral species show higher
190 speciation rates (although lower overall diversification rates) compared to nocturnal and
191 diurnal species²⁴. If these patterns are also true for the rest of Mammalia, they could explain
192 the persistence of mammal cathemerality against the net outflow of species and slow
193 diversification rates. In Lepidoptera (moths and butterflies), the persistence of a mixed
194 (cathemeral) diel activity pattern has been argued to be the result of conflicting predation
195 pressures, from bats during the night and birds during the day⁴². Hence, cathemeral activity
196 may be preferred when strong selective forces are acting at opposite directions. The
197 appearance of mammal cathemerality may have been due to high nocturnal predation risk,
198 perhaps from other mammals that would have made the nocturnal niche less advantageous.

199 The higher transition rates for the LF tree are likely a result of the method we used to
200 construct the species-level LF phylogeny, i.e. re-scaling the branch lengths of species-level
201 clades from the SF phylogeny²⁸ to maintain the length of the corresponding terminal branch
202 provided by²⁷. SF branch lengths were usually scaled down in this process, because the SF
203 generally estimates older divergence dates than the LF, reflecting the difference between the
204 two phylogenetic models. A consequence of our grafting procedure is that a band of
205 artificially short branches is formed near these graft points, which implies rapid change.
206 Higher rates allow for more change along tree branches, and reduce the precision of the
207 results, which probably contributed to our LF reconstruction yielding fewer decisive
208 predictions and lower statistical support compared with the SF reconstruction (Figs. 2, 3 and
209 4). Whilst a direct comparison of transition rates between the two phylogenetic hypotheses is
210 therefore precluded, the broad pattern of transitions (i.e. low transition rates into
211 cathemerality and high transition rates out of it in either direction) is supported in both

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212 analyses, as is the general pattern of temporal niche evolution that emerges from the node
213 reconstructions.

214 Although we have demonstrated the importance of the phylogenetic comparative
215 approach to the investigation of the evolution of behavioural traits in mammals, ancestral
216 reconstruction methods rely heavily on the accuracy of phylogenetic estimates. The LF
217 hypothesis of mammalian evolutionary history is well supported^{27,37,40}, but phylogenetic
218 estimates are only available at family-level, and further modification was required to add the
219 species-level information for our analysis. Despite the attention attracted recently by studies
220 of mammalian phylogenies^{27,37,40,43}, only the SF hypothesis is represented by a species-level
221 phylogeny, making the incorporation of the LF hypothesis and the explosive model
222 problematic for phylogenetic comparative analyses that are based on detailed species-level
223 data.

224 In conclusion, we argue that the activity patterns of Mesozoic mammals are consistent
225 with the prediction of temporal partitioning, and that the gradual acquisition of daytime
226 activity in mammals, first cathemerality then diurnality, coincided with the decrease in
227 pressure from dinosaurs, whether due to their decline or extinction. Given the current
228 evidence, temporal partitioning within Mesozoic amniotes mostly followed the phylogenetic
229 (mammal-archosaur) division, but while some dinosaurs invaded the nocturnal niche⁴⁴, we
230 find little support for Mesozoic mammals invading the diurnal niche. The constraints on
231 mammals becoming diurnal during the Mesozoic would have been strong enough to
232 counteract the ecological pressure to diversify, following at least 100Myr of mammalian
233 sensory and eco-morphological radiations that sub-divided their nocturnal niches. Mammals
234 diversified rapidly once they expanded outside the nocturnal niche, but whether invading the
235 diurnal niche facilitated mammals' Cenozoic success remains to be answered.

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236 **Methods**

237 **Data.** We collated activity records for 2415 mammal species, representing all 29
238 extant orders and 135 of 148 extant families from the PanTHERIA database¹, and from
239 published sources such as research articles, field guides, and encyclopaedias (Supplementary
240 Table 1). Data collection was designed to incorporate extensive phylogenetic diversity,
241 seeking to represent maximum ordinal diversity before targeting familial and generic
242 diversity. We assigned each species into one of five activity patterns: (i) nocturnal – active
243 only or mostly in the dark; (ii) diurnal – active only or mostly during daylight hours; (iii)
244 cathemeral – active both during the day and during the night; (iv) crepuscular – active only at
245 twilight, around sunrise and/or sunset; and (v) ultradian – active in cycles of a few hours. We
246 follow the taxonomy and species binomials in Mammal Species of the World, 3rd Edition⁴⁵,
247 with one exception: we use Cetartiodactyla, instead of separate orders Artiodactyla and
248 Cetacea, following^{46,47}. We resolved conflicts where sources disagreed on species activity
249 pattern as follows: (i) records with a combination of either nocturnal and crepuscular, or
250 diurnal and crepuscular were changed to nocturnal or diurnal, respectively; (ii) records from
251 compiled sources were preferred over localised studies (which are prone to idiosyncrasies);
252 and (iii) records from more recent sources were preferred. This left 29 species unresolved and
253 these species were excluded from subsequent analyses.

254 **Phylogenetic framework.** We used two phylogenetic frameworks representing two
255 of the main hypotheses of mammalian evolutionary history for our analyses: the short-fuse
256 (SF) hypothesis is represented by the species-level "best dates" supertree²⁸ updated from²⁹,
257 and the long-fuse (LF) hypothesis is represented by the amino-acid supermatrix phylogeny²⁷
258 (Fig.1). The SF hypothesis asserts that the most recent common ancestor (MRCA) of all
259 extant mammals diverged into its daughter lineages (Prototheria and Theria) in the mid-
260 Jurassic, 166.2Mya, whereas according to the LF hypothesis this divergence took place in the

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261 late-Triassic, 217.8Mya. Both hypotheses agree that multiple extant lineages diverged in the
262 Cretaceous and survived the K-Pg event (Fig. 1), but the SF hypothesis posits that intra-
263 ordinal divergence of placental mammals had already begun prior to the K-Pg event, while
264 the LF hypothesis places intra-ordinal divergence in the Cenozoic. A third evolutionary
265 hypothesis, the explosive model, is supported by fossil evidence and morphological data⁴³,
266 but has been criticised for implying impossibly-high rates of evolution in the early-Cenozoic
267 radiation of placental mammals, and for other problems^{37,48}, so we do not consider it here.

268 Here, we represent the LF hypothesis using the family-level supermatrix phylogeny²⁷
269 (downloaded from TreeBASE: <http://purl.org/phylo/treebase/phylovs/study/TB2:S11872> on
270 01MAR2015). For our analyses we rendered it ultrametric, i.e. all the tips (species) of the tree
271 are equidistant from the root, so that branch lengths are proportional to time. The LF
272 hypothesis has recently gained support from several studies³⁷⁻⁴⁰, but it lacks species-level
273 resolution, which is essential for our analysis. We therefore used each terminal branch of the
274 supermatrix phylogeny (representing a taxonomic family) as a root branch onto which we
275 appended the internal branching pattern of the family, as given in²⁸ updated from²⁹. In order
276 to retain the original LF timeline, we scaled the appended branching pattern to 85% of its
277 original supermatrix phylogeny branch length, and the root branch completed the remaining
278 15%. For this process we used functions from packages *ape*⁴⁹ and *phangorn*⁵⁰ in R version
279 3.2.3⁵¹. Species that we had data for but that were absent from the phylogenetic frameworks
280 were omitted from the analyses: 33 species from the SF phylogeny, and an additional 38
281 species missing from the LF phylogeny as families Aotidae, Pitheciidae and Lepilemuridae
282 (Primates) were not originally included in the supermatrix phylogeny²⁷. Thus, our analyses
283 consist of 60% nocturnal species (n = 1399 species; n = 1384 species for SF and LF
284 phylogenies, respectively), 14% cathemeral species (n = 321 species SF; n = 320 species LF),
285 and 26% diurnal species (n = 610 species SF; n = 588 species LF).

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286 **Analyses.** We used *BayesTraits* v3³⁰ to reconstruct the evolution of mammalian
287 activity patterns. *BayesTraits* implements Markov Chain Monte Carlo (MCMC) methods to
288 sample from the posterior distributions of transition rates for a transition matrix describing
289 the evolution of a discrete character. The obtained posterior distribution allows the user to
290 infer the posterior probability of each character state at the root and at each internal node of
291 the phylogeny. By employing reversible jump MCMC (rjMCMC), *BayesTraits* is also able to
292 sample from the posterior distribution of model configurations and optimise the number of
293 parameters in the model. This removes the need for comparing models with different number
294 of parameters by sampling from model space and parameter space concurrently⁵². We only
295 consider the three main activity patterns across mammals in our analysis (nocturnal n = 1932
296 species, diurnal n = 999, and cathemeral n = 415, Supplementary Table 1) in order to reduce
297 the complexity of the model and increase its biological interpretability (four transition rates
298 instead of 16). Additionally, we do not consider ultradian activity patterns as these are mostly
299 found with polar and subterranean species, where the 24-hour cycle is of reduced importance.
300 We consider an ordered model of trait evolution: Nocturnal↔Cathemeral↔Diurnal, whereby
301 direct Nocturnal↔Diurnal transitions are not allowed (set to zero), because morphological
302 and histological adaptations to diurnality and nocturnality are mutually exclusive, while
303 cathemerality involves an intermediate state of the relevant phenotypes^{20,53}. Our underlying
304 hypothesis is that during shifts from diurnality to nocturnality (or vice versa) species go
305 through a phase where they are equally well adapted to both. All other transition rates were
306 free to take any value. We used rjMCMC to estimate the optimal model configuration⁵². As
307 activity pattern in our analyses was not a binary trait, we used the ‘multistate’ mode of
308 *BayesTraits* to sample from the posterior distribution of transition rates between activity
309 pattern categories. For each phylogeny, we opted for the reversible-jump MCMC procedure,
310 and set a wide uniform prior, bounded between 0 and 100 for all transition rates, to ensure

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311 that our prior did not have a strong effect on the nature of the posterior. Each rjMCMC chain
312 was run until convergence was reached (at least one million iterations), after which point the
313 chains were sampled every 4000 iterations until a posterior of 1000 samples was obtained.
314 We chose this wide sampling interval in order to minimise autocorrelation in our posterior
315 samples. We ran twelve replicates of each chain (corresponding a phylogeny) in order to
316 ensure consistency, and that each independent run converged on the same posterior
317 distribution. The marginal likelihoods of each chain were calculated using the stepping stone
318 sampler⁵⁴ as implemented in *BayesTraits* (500 stones, 1000 iterations per stone) and
319 compared between independent replicates to ensure consistency. In order to estimate the
320 character state at each internal node, we used the modal value of the PP of each character
321 state, calculated as the peak value of the kernel density of each posterior distribution. We
322 used the R package *phytools*⁵⁵ to plot the PP values of each node on the mammal
323 phylogenies (Figs. 3 and 4). To measure the accumulation of mammalian temporal niches
324 over time, we calculated the running total of nodes (lineages) where an activity pattern was
325 supported with $PP > 0.67$, and plotted this along the mammal evolution timeline (Figs. 3 and
326 4). The confidence threshold of 0.67 was chosen because an activity pattern supported at this
327 level would mean that the next most likely pattern is less than half as likely.

328 **Data Availability.** The authors declare that all data supporting the findings of this study are
329 available within the paper and its supplementary information files. All data have been
330 deposited on Figshare and will be made publically available after manuscript acceptance (doi:
331 [10.6084/m9.figshare.4775416](https://doi.org/10.6084/m9.figshare.4775416); doi:10.6084/m9.figshare.4774648). Reprints and permissions
332 information are available at www.nature.com/reprints.

333 **Code Availability.** Computer code essential for replicating the results in this study has been
334 deposited on Figshare and will be made publicly available after manuscript acceptance (doi:
335 [10.6084/m9.figshare.4797367](https://doi.org/10.6084/m9.figshare.4797367)).

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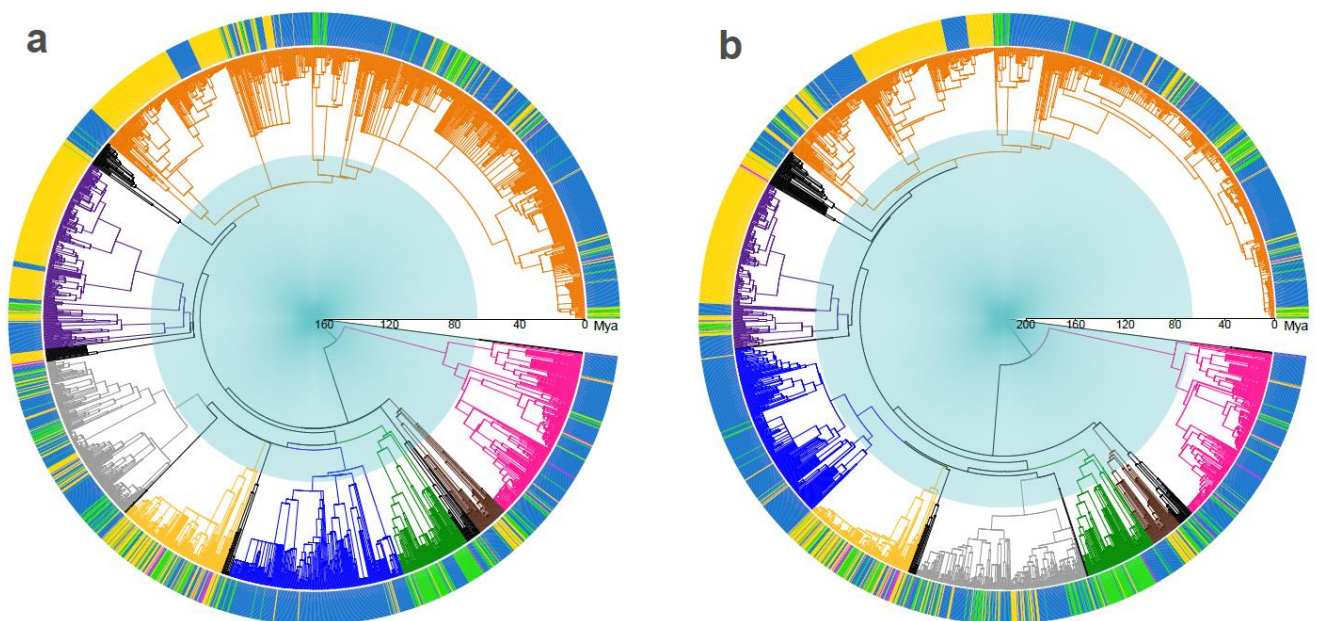
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500 **Author Information** The authors declare no competing financial interests. Correspondence
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503 **Figure 1. Activity patterns distribution across (a) the short-fuse (SF), and (b) the long-**
504 **fuse (LF) estimates of mammalian evolution.** Species activity patterns are denoted by
505 different colours in the perimeter circle, where nocturnal is denoted as blue; diurnal yellow;
506 cathemeral green; and ambiguous magenta. Branch colours represent taxonomy, where
507 Marsupials are pink; Afrotheria brown; Soricomorpha+Erinaceomorpha green; Chiroptera
508 blue; Cetartiodactyla yellow; Carnivora grey; Primates purple; Rodentia orange; and all other
509 orders are black. Mesozoic and Cenozoic eras are denoted by blue and white backgrounds,
510 respectively. SF phylogeny follows²⁸ updated by²⁹, and LF phylogeny is adapted from²⁷ (see
511 Methods). Branch lengths are proportional to time (Myr).

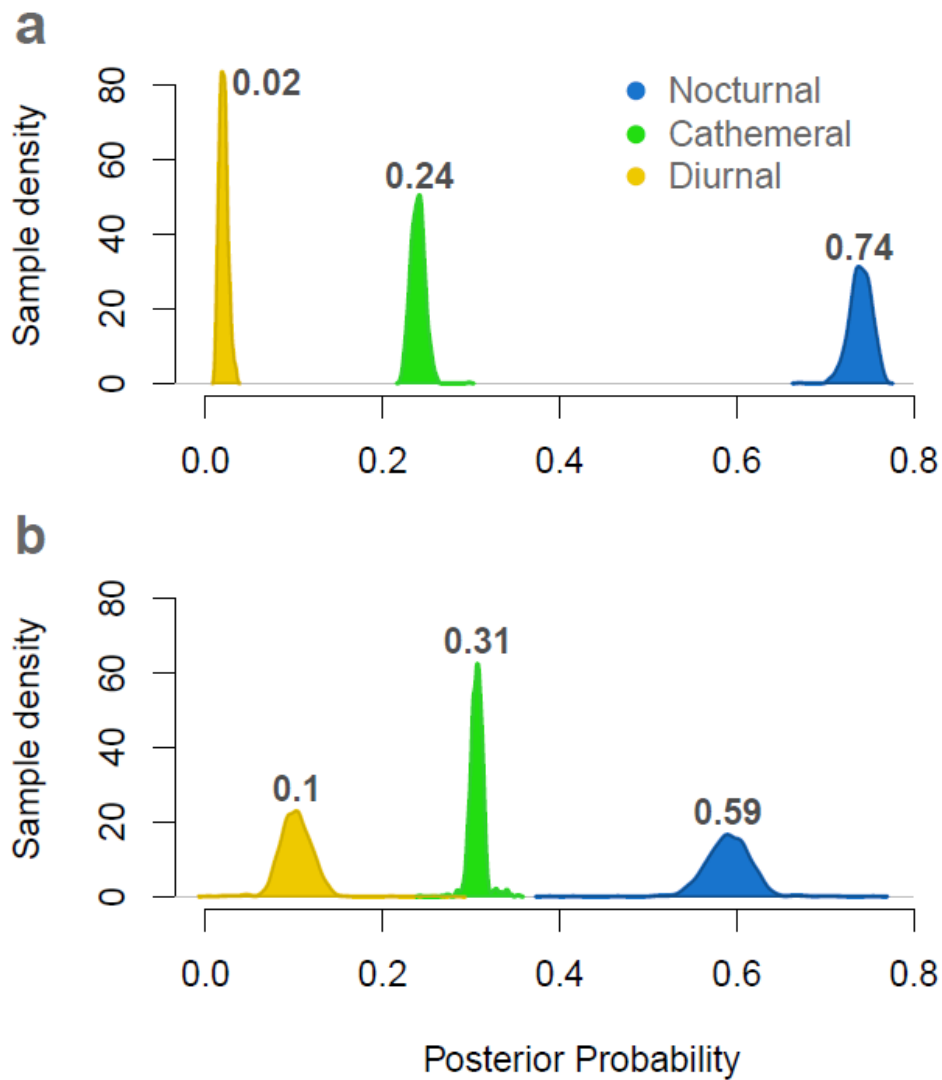
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514 **Figure 2. Posterior probability (PP) density of ancestral activity patterns**
515 **reconstructions of the most recent common ancestor of crown-group Mammalia from**
516 **(a) SF and (b) LF phylogenies.** Distribution curves are calculated from 1000 post-burnin
517 rjMCMC samples, and modal PP values for each distribution are shown in bold. Colours
518 correspond to activity patterns.



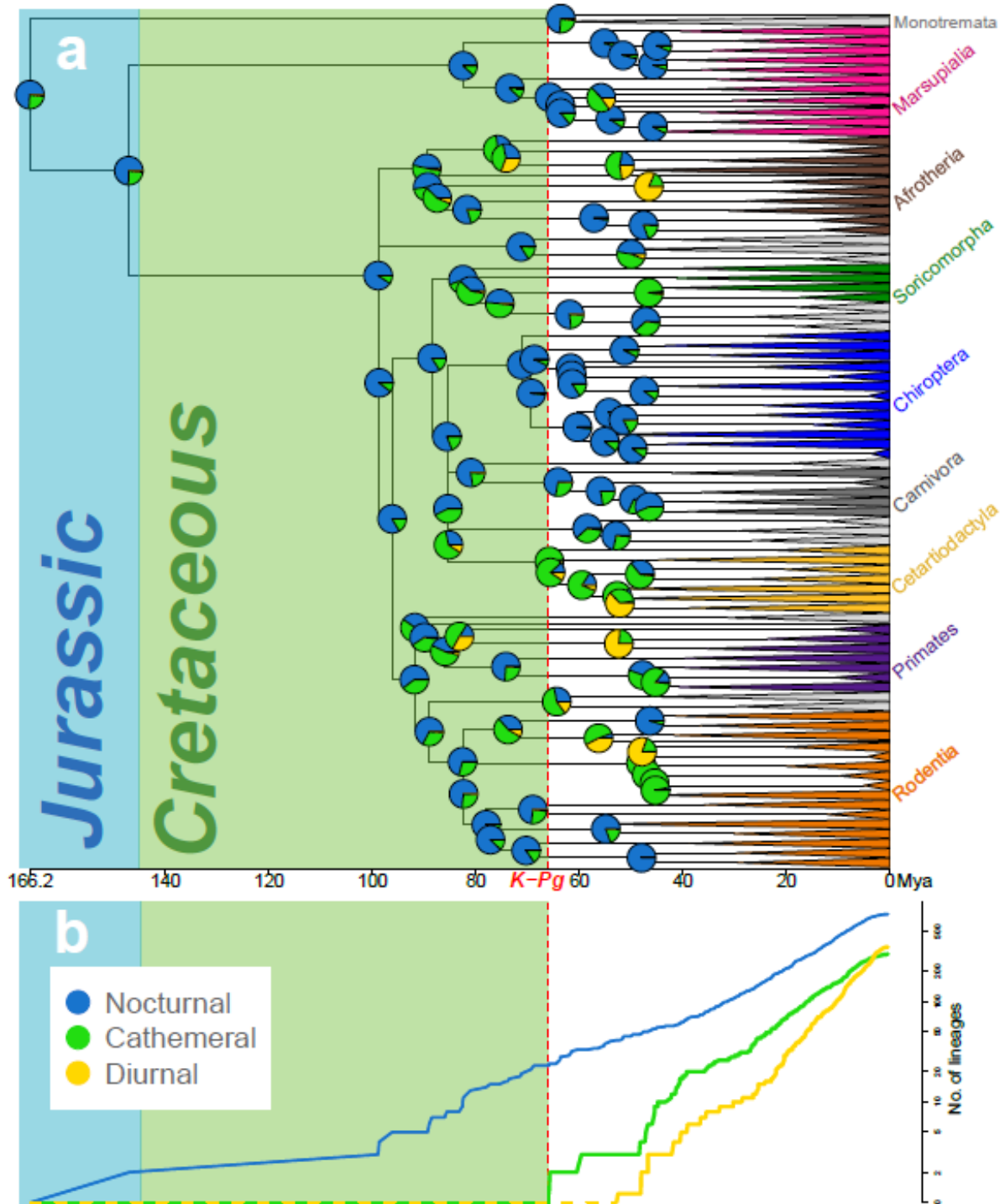
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521 **Figure 3. Reconstruction of ancestral activity patterns and character accumulation,**
522 **across the ‘short fuse’ (SF) hypothesis of mammalian evolution.** (a) Ancestral activity
523 pattern reconstruction across the SF phylogeny²⁸ updated by²⁹. Pie charts correspond to
524 ancestral reconstructions at each node, and colours denote the proportional value of the
525 posterior probability (PP) of each activity pattern, where nocturnal is blue; cathemeral green;
526 and diurnal yellow. Shading denotes geological era. Branch lengths are proportional to time,
527 with branches younger than 45Mya replaced with wedges for visualisation purposes. The red
528 dashed line represents the K-Pg boundary. (b) Lineages through time plot for activity
529 patterns. The predominant activity pattern was assigned to each node based on PP values,
530 with a minimum value of 0.67. Nodes with reconstructed activity pattern PP values of <0.67
531 were excluded from the lineages through time plot.

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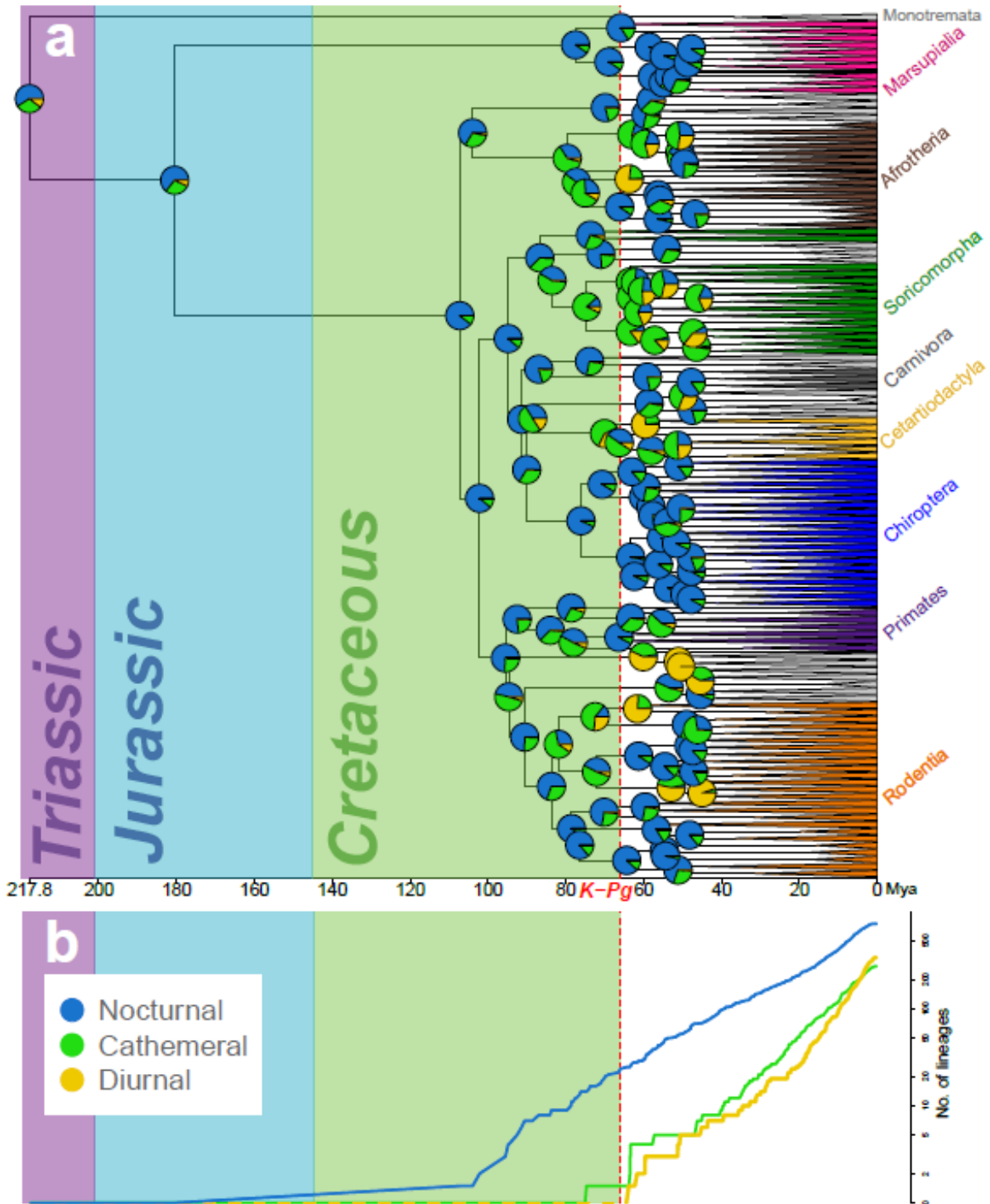


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533 **Figure 4. Reconstruction of ancestral activity patterns and character accumulation,**
534 **across the ‘long fuse’ (LF) hypothesis of mammalian evolution.** (a) Ancestral activity
535 pattern reconstruction across the LF phylogeny adapted from²⁷. Pie charts correspond to
536 ancestral reconstructions at each node, and colours denote the proportional value of the
537 posterior probability (PP) of each activity pattern, where nocturnal is blue; cathemeral green;
538 and diurnal yellow. Shading denotes geological era. Branch lengths are proportional to time,
539 with branches younger than 45Mya replaced with wedges for visualisation purposes. The red
540 dashed line represents the K-Pg boundary. (b) Lineages through time plot for activity
541 patterns. The predominant activity pattern was assigned to each node based on PP values,
542 with a minimum value of 0.67. Nodes with reconstructed activity pattern PP values of <0.67
543 were excluded from the lineages through time plot.

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545 **Table 1. Character transition rate matrix for SF and LF ancestral activity pattern**
546 **reconstructions.** Transition rates are from the state in the column to the state in the row and
547 represent model posterior values. Direct transitions between nocturnal and diurnal were not
548 allowed (0) under our character state transition model.

549

Phylogeny		Transition rates		
		Nocturnal	Cathemeral	Diurnal
Short fuse	Nocturnal	-	0.01	0
	Cathemeral	0.03	-	0.03
	Diurnal	0	0.01	-
Long fuse	Nocturnal	-	1.97	0
	Cathemeral	7.46	-	7.41
	Diurnal	0	1.96	-

550