

# *Rapid change in mammalian eye shape is explained by activity pattern*

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1 **Rapid change in mammalian eye shape is explained by**  
2 **activity pattern**

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## 7 **Summary**

8 The rate of morphological evolution along the branches of a phylogeny varies widely  
9 [1-6]. Although such rate variation is often assumed to reflect the strength of historical  
10 natural selection resulting in adaptation [7-14], this lacks empirical and analytical  
11 evidence. One way to demonstrate a relationship between branchwise rates and  
12 adaptation would be to show that rapid rates of evolution are linked with ecological  
13 shifts or key innovations. Here we test for this link by determining whether activity  
14 pattern – the time of day at which species are active – explains rapid bursts of  
15 evolutionary change in eye shape. Using modern approaches to identify shifts in the  
16 rate of morphological evolution [7, 13], we find that over 74% of rapid eye shape  
17 change during mammalian evolutionary history is directly explained by distinct  
18 selection pressures acting on nocturnal, cathemeral, and diurnal species. Our results  
19 reveal how ecological changes occurring along the branches of a phylogeny can  
20 manifest in subsequent changes in the rate of morphological evolution. Although  
21 selective pressures exerted by different activity patterns have acted uniformly across  
22 all mammals, we find differences in the rate of eye shape evolution among orders. The  
23 key to understanding this is in how ecology itself has evolved. We find heterogeneity  
24 in how activity pattern has evolved among mammals that ultimately led to differences  
25 in the rate of eye shape evolution among species. Our approach represents an exciting  
26 new way to pinpoint factors driving adaptation, enabling a clearer understanding of  
27 what factors drive the evolution of biological diversity.

28 **Keywords**

29 Morphological Rates, Phylogeny, Comparative Methods, Natural Selection, Activity  
30 Pattern, Eye shape

31 **Results and Discussion**

32 We test whether rapid shifts in the rate of morphological evolution can be linked to an  
33 underlying ecological cause. We used the phylogenetic variable-rates regression  
34 model [7] to test for variation in the rate of eye shape evolution across the mammal  
35 phylogeny [15] whilst also estimating the relationship between corneal diameter (a  
36 proxy for pupil size) and axial eye length (a proxy for focal distance). This relationship  
37 has previously been used to summarize eye shape [e.g. 16, 17] (Figure 1). The  
38 variable-rates regression model works within a Bayesian Markov chain Monte Carlo  
39 (MCMC) framework to estimate a posterior distribution of the rate of evolution along  
40 each individual branch of the phylogeny ( $r$ ) and an underlying global background rate  
41 of change (STAR Methods) [7, 13]. We define rate shifts where the posterior  
42 distribution of estimated  $r$  for a branch exceeds 1 in  $\geq 95\%$  of the posterior distribution.  
43 In these cases, the branch is evolving at a faster rate compared to the background  
44 rate of evolution, and there is significant unexplained residual variance away from the  
45 estimated underlying evolutionary relationship.

46 In our bivariate variable-rates regression between corneal diameter and axial length  
47 (henceforth *simple eye shape model*), we find a significantly positive slope in the eye  
48 shape relationship (judged by the proportion of the posterior distribution crossing zero  
49 [ $P_x$ ] = 0, Figure 2a, Table S1) and there is significant rate heterogeneity (Bayes Factor  
50 [ $BF$ ] = 520.438 compared to a regression model that estimates only a single  
51 background rate, see STAR methods). We identify a total of 128 branches as

52 significant rate shifts ( $n_{rapid} = 128$ , Figure 2a) out of a total of 508 branches ( $n_{total} =$   
53 508, 25.2% of all branches have had rapid shifts in the rate of eye shape change).  
54 These fall predominantly within carnivores ( $n_{rapid} = 74$ , modal  $r$  range = 5.16-10.20)  
55 and anthropoid primates ( $n_{rapid} = 44$ , modal  $r$  range 3.49-6.95) but also along  
56 branches leading to two pangolin species ( $n_{rapid} = 3$ , modal  $r$  range = 6.37-12.05),  
57 the woodchuck (modal  $r = 6.59$ ), the greater hedgehog tenrec (modal  $r = 4.04$ ) and  
58 three species of *Equus* ( $n_{rapid} = 5$ , modal  $r$  range = 5.62-6.42). 100% of branches  
59 within carnivores and 54% within anthropoid primates are identified as rapid rate shifts.  
60 Such rapid shifts in the rate of morphological evolution (Figure 2a) are often used to  
61 identify episodes of exceptional change, where the magnitude of the rate shift is  
62 implicitly associated with the strength of historical selection pressures [7-14]. However,  
63 there is no current statistical evidence for this interpretation of rapid rates. One way to  
64 demonstrate that branch-wise rates of morphological evolution reflect selection  
65 pressures driving adaptation across millions of years would be to show that branches  
66 undergoing rapid rates of morphological evolution are associated with shifts in  
67 ecology, key innovations or increased ecological opportunity [14] (Figure 3). Here, we  
68 use the phylogenetic variable rates regression framework to test whether activity  
69 pattern (the time of day at which species are active) can explain shifts in the rate of  
70 evolution in mammalian eye shape.

71 Among vertebrates, there is an established association between activity pattern and  
72 eye shape [18-21]. Nocturnal vertebrates tend to maximize light sensitivity with larger  
73 pupils [20-22], whereas diurnal species facilitate visual acuity with longer focal  
74 distances (i.e. longer eyes relative to pupils) [20, 21, 23, 24]. Cathemeral species show  
75 adaptations to unspecialised lifestyles, resulting in some intermediate eye shape [22,

76 25]. We expect activity pattern to be a primary driver of mammalian eye shape  
77 evolution as it is in other vertebrates [25, 26], and it should be possible to detect this  
78 using rates of evolution. In the variable-rates framework, rapid rates shifts arise as a  
79 consequence of significant unexplained residual variance away from the estimated  
80 underlying evolutionary relationship. If activity pattern was the primary selection  
81 pressure on eye shape in the 128 branches we identify as rapid rate shifts (Figure 2a),  
82 then including activity pattern as an additional explanatory factor into the simple eye  
83 shape variable-rates regression model would result in all rate shifts disappearing  
84 (Figure 3). This would be because activity pattern explains the exceptional deviations  
85 away from the underlying eye shape relationship (i.e. the 128 rate shifts). That is,  
86 activity pattern would reduce the previously unexplained phylogenetically structured  
87 residual variance in eye shape (see STAR Methods and Figure 3).

88 In a variable-rates regression model that allows each activity pattern to have a different  
89 slope in the eye shape relationship (*activity pattern model*), we find that the  
90 relationship is sharpest in nocturnal mammals ( $\beta = 0.904$ , Figure 2, Table S1). In line  
91 with other vertebrates, [18-21, 26], the slope is shallowest in diurnal mammals ( $\beta =$   
92  $0.810$ ), and cathemeral species have a moderate slope ( $\beta = 0.698$ , Figure 2, Table  
93 S1). This demonstrates a significantly increasing slope in the relationship between  
94 corneal diameter and axial length with reducing amounts of daylight activity. That is,  
95 nocturnal species increase their relative corneal size more with increasing eye length  
96 than diurnal species across the same range of eye lengths (Figure 2B). That is, a  
97 large-eyed diurnal species will have relatively clearer vision than a nocturnal species  
98 with an eye of the same size – which will instead maximize image brightness.

99 In the activity pattern model, we still find significant rate heterogeneity ( $BF = 521.500$ ),  
100 but overall, there is a 74.2% reduction in the number of branches identified as rate

101 shifts ( $n_{rapid} = 33$ , see Table S2 for details) compared to the simple eye shape model  
102 (Figure 2). Therefore, 95 branches have undergone what we will term *activity pattern*  
103 *driven* episodes of rapid eye shape evolution, explained by the different evolutionary  
104 slopes in the relationship between corneal diameter and eye length in the activity  
105 pattern model (Figure 2).

106 Mammals have large overlap in eye morphology among species of different activity  
107 patterns (Figure 1) and are often reported to have eyes similar to other nocturnal  
108 vertebrates [16, 17]. This ‘nocturnal’ eye shape and an associated reduction in  
109 morphological diversity among mammals is thought to have arisen (along with other  
110 adaptations [16, 27, 28]) during a long period of life in the dark early in mammalian  
111 history – a *nocturnal bottleneck*. This prolonged adaptation to nocturnality has led  
112 some authors to suggest that changes in activity pattern later in evolution may not  
113 have provided sufficient selection pressures to change eye shapes in the expected  
114 way [16]. However, we find 95 activity pattern driven episodes of eye shape evolution  
115 (Figure 1). Even in the case that incipient mammals underwent an early nocturnal  
116 bottleneck, beyond their nocturnal origins there has been more than 160 million years  
117 of independent eye shape evolution. The results of our variable rates regressions  
118 reveal that during this time, over 74% of all branches with rapid rate shifts in eye shape  
119 evolution can be directly explained by activity pattern.

120 Our results are consistent with predictions made by adaptive hypotheses, and provide  
121 the first analytical evidence for the previously implicit idea [7-13] that intense and rapid  
122 bursts of evolution can be attributed to historical natural selection.

123 Anthropoid primates are often heralded as unique in terms of their eye shape; they  
124 have relatively reduced corneal diameters compared to other mammals and thus  
125 relatively high visual acuity [e.g. 29, 30] (Figure 1). Notably, the branch leading to the

126 only nocturnal anthropoid primate, *Aotus*, is one of the activity pattern driven episodes  
127 of rapid eye shape evolution we find here; owl monkeys rapidly changed their eye  
128 shape in order to adapt to their exclusively reverted nocturnal niche. All other  
129 anthropoid primates are diurnal. A transition to diurnality in combination with  
130 behaviours heavily dependent on vision (such as visual predation) is commonly  
131 invoked as an explanation for the origin of the unique anthropoid morphology [31-33].  
132 This suggests that both diet and activity pattern might have driven rapid changes in  
133 eye shape observed along the branch leading to anthropoid primates. Our variable  
134 rates regression model demonstrates that activity pattern, at least, did play a key role  
135 in this transition: there is a rapid shift in the rate of eye shape change observed along  
136 the branch at the base of anthropoid primates that is completely explained by the eye  
137 shape slope estimated for all diurnal mammals (Figure 2). However, although the  
138 relatively reduced corneal sizes of anthropoids is associated with a shift to diurnality,  
139 this group is not special or unique. With the exception of Papionini (drills, mangabeys,  
140 and baboons) and the moustached tamarin (see Table S2, Figure 2), the reduction in  
141 corneal diameter observed among anthropoid primates is *expected* given their  
142 phylogenetic position and their activity pattern.

143 If activity pattern drives eye shape uniformly across mammals, then why do we  
144 observe different patterns in the rate of eye shape change among orders? The key to  
145 understanding this may be in how activity pattern itself has evolved. In order to  
146 reconstruct the evolutionary history of mammalian activity pattern, we estimated  
147 discrete transition rates among activity patterns (defined as the rate of switching  
148 between different states along individual branches of a phylogenetic tree) using a  
149 Continuous-time Markov transition model [34] allowing all transition rates to vary  
150 implemented within a Bayesian framework [35] (henceforth referred to as *transition-*



151 *rates models*). Analyses of transition rates among mammalian activity patterns are  
152 scant [cf. 36, 37, 38], and often limited in taxonomic scope [cf. 39]. We therefore  
153 expanded our transition-rates models to include all mammals with available activity  
154 pattern data (N = 3014, STAR Methods). Across all mammals, our results do not  
155 support the recent suggestion that there has been no direct transitions between  
156 nocturnal and diurnal lifestyles [39] (Figure 4a). Otherwise, transitions away from  
157 cathemeral lifestyles occur more frequently than those towards cathemeral  
158 (supporting recent results using a smaller dataset [39]).

159 Estimating a single pattern of transition rates across all mammals in this way is fraught  
160 with danger – when we estimate transition rates separately across all large orders of  
161 mammals, we find substantial differences in not only the pattern of transitions (Figure  
162 4b-d, Figure S1) but also the overall speed of activity pattern change [40] (Figure 4b-  
163 d). This highlights that the emergent pattern in transitions across all mammals is likely  
164 to be a meta-phenomenon which is difficult to interpret biologically. The previously  
165 unappreciated non-uniformity in pattern and speed of activity pattern transitions is  
166 interesting. While a formal analysis is beyond the scope of this study, it suggests that  
167 the underlying drivers and mechanisms associated with these transitions are variable  
168 – potentially associated with the varied environmental and ecological pressures facing  
169 species within different mammalian orders.

170 With this in mind, direct transitions between nocturnality and diurnality are rare in  
171 several orders (e.g. Lagomorpha and Eulipotyphla, Figure S1). This is in support of  
172 the suggestion that transitions between diurnal and nocturnal lifestyles must pass  
173 through an “intermediate” cathemeral phase [39]. However, although cathemeral eyes  
174 are expected to have an “intermediate” shape between nocturnal and diurnal species  
175 [22, 25], there is no particular reason to assume that it is impossible for species to

176 move from day- to night-living or vice versa. Such transitions are supported in both  
177 carnivores and rodents (Figure 4). In general, heterogeneity in activity pattern  
178 evolution such as that revealed by our transition rates analysis (Figure 3) may  
179 ultimately be the underlying driver of heterogeneity in eye shape evolution (Figure 4).  
180 Fundamental differences in ecology and how ecology has evolved among taxa has  
181 the potential to explain why we observe different rates of continuous morphological  
182 change among orders (in our variable rates regression models). Because eye shape  
183 and activity pattern are linked (Figure 2), where activity pattern has evolved rapidly –  
184 with many transitions between states in a short period of time (e.g. carnivores, Figure  
185 3b inset) – it would necessarily result in rapid rates of eye shape evolution (Figure 4).  
186 For now, there is a lack of approaches allowing us to characterize and incorporate  
187 heterogeneity of transition rates among ecological characters within clades of  
188 organisms – or even along individual branches of a phylogenetic tree – into our models  
189 of discrete character evolution. Assuming simple directionality away from nocturnality  
190 or allowing only a single pattern across all mammals [38, 39] in the face of this  
191 heterogeneity (Figures 2, 3) can hinder our ability to infer ancestral forms, and so we  
192 do not say anything about nor do we attempt to estimate the ancestral condition of  
193 mammals here.

194 Fortunately, difficulties associated with ancestral state reconstruction or confirming  
195 whether or not the earliest mammals were nocturnal has absolutely no bearing on the  
196 selection pressures faced by different species as they evolved specializations and  
197 adaptations beyond those faced by the first mammals millions of years ago.  
198 Regardless of whether the ancestral mammal was nocturnal [16, 17, 38, 39] or as  
199 some authors have recently suggested, cathemeral [37, 41, 42], as mammals evolved

200 and diversified, natural selection acted to sculpt their morphology in different and  
201 important ways.

202 Here, we highlight a new way to determine which factors drive exceptional bursts of  
203 phenotypic evolution. Although activity pattern can explain most rapid evolutionary  
204 change in eye shape, there are 33 rapid shifts in the rate of mammalian eye shape  
205 evolution that remain unexplained (Table S2). In these cases, other factors such as  
206 brain size [43, 44], running speed [45], diet [24], or environment [46] must have  
207 imposed different and more important selection pressures on eye shape. Fortunately,  
208 the approach we describe here provides the potential to test for the influence of those  
209 other factors as the data become available.

210 Beyond the mammalian eye, placing rates of continuous morphological change within  
211 an explicitly ecological context provides a framework that offers researchers a way to  
212 analyse links between ecology and morphology even in the absence of directional  
213 change. Taken together, our approach provides the opportunity to obtain a deeper  
214 understanding of what factors truly drive the evolution of biological diversity.

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## 220 **Author Contributions**

221 Both authors contributed to all aspects of this work, including writing the paper.

## 222 **Declaration of Interests**

223 The authors declare no competing interests.

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373

374 **Figure Titles and Legends**

375 **Figure 1: Mammalian eye shape.** A bivariate plot depicting mammal eye shape (n =  
376 266) as the relationship between corneal diameter (a proxy for pupil size) and axial  
377 eye length (a proxy for focal distance). Colours indicate activity pattern (see legend).  
378 Anthropoid primates are shown as squares; all other species are shown as circles.  
379 This plot must be interpreted with caution; data points are not independent owing to  
380 shared ancestry.

381 **Figure 2: The effect of activity pattern on the rate of eye shape evolution.**  
382 Branches of the mammal phylogeny (n = 266) along which there have been rapid rate  
383 shifts ( $r > 1$  in  $\geq 95\%$  of the posterior distribution) in the simple eye shape model (a) and  
384 the activity pattern model (b) are stretched to represent their median rate of evolution  
385 (i.e. longer branches have faster rates) and are coloured by group. The branch leading  
386 to anthropoid primates is marked with an arrow. All other branches are measured in  
387 millions of years. The posterior predicted phylogenetic slopes are shown in (a, inset)  
388 for the simple eye shape model and in (b, inset bottom) for the activity pattern model  
389 – the median predicted slope is highlighted. Pairwise comparisons between the  
390 magnitudes of each slope are given in (b, inset top) as the posterior distributions of  
391 differences between two estimated  $\beta$  parameters. The nocturnal slope is significantly  
392 different to both the cathemeral ( $P_{x[diff]} = 0.045$ ) and the diurnal slopes ( $P_{x[diff]} =$   
393 0.003). The diurnal slope is the shallowest and is significantly shallower than the  
394 cathemeral slope ( $P_{x[diff]} = 0.031$ ). See also Table S1 for parameter values and Table  
395 S2 for details on rate shifts that remain unexplained by activity pattern.

396 **Figure 3: A schematic of how we can reveal the underlying causes of rate**  
397 **variation.** (a) A phylogeny with branches measured in millions of years. (b) Tests for

398 rate heterogeneity on this phylogeny in combination with eye shape data for species  
399 at the terminal branches reveals multiple rate shifts along individual branches in the  
400 tree (exceptionally rapid rates of evolutionary change arising from significant  
401 unexplained phylogenetic residual variance in the eye shape relationship). These  
402 branches are coloured black and are stretched according to their rate of evolution  
403 (longer branches = faster rates). All other branches have evolved as expected given  
404 their length in time i.e. they are encompassed within the variation explained by the  
405 underlying regression relationship in combination with the overall background rate of  
406 eye shape change acting across all mammals. We show two potential scenarios with  
407 extreme outcomes of including activity pattern into tests for rate variation (yellow =  
408 diurnal, green = cathemeral, blue = nocturnal). (c) In the first scenario, natural  
409 selection on eye shape has been driven exclusively by activity pattern. All rapid bursts  
410 of change in eye shape evolution – all rate shifts – can therefore be explained by the  
411 inclusion of activity pattern into the model i.e. no branches remain stretched. (d) In the  
412 second scenario, activity pattern is randomly distributed with regards to eye shape and  
413 so all rate shifts remain identified as instances of significant and substantial  
414 unexplained variation in eye shape (black, stretched branches). That is, activity pattern  
415 does not explain any of the unexplained phylogenetic residual variance in eye shape  
416 that manifests as rapid rate shifts. Note that here, eye shape variation is represented  
417 by pupil size– in reality, it is *relative* pupil size that is important.

418

419 **Figure 4: Transition rates amongst activity patterns in mammals and the three**  
420 **largest orders.** The results of our discrete transition analyses across all mammals (n  
421 = 3014). In all cases, pairwise transitions between activity patterns are indicated by  
422 the directions of the arrows and each transition rate is shown as a density distribution

423 in a corresponding colour. Activity patterns are indicated by the letters and coloured  
424 boxes where N (blue) = nocturnal, C (green) = cathemeral/crepuscular and D (yellow)  
425 = diurnal. Each arrow is shaded to match the corresponding distribution of estimated  
426 transition rates. Results are shown for a model run across (a) all mammals, n = 3014  
427 (b) carnivores, n = 236 (c) primates, n = 301 and (d) rodents, n = 1098. Inset for each  
428 of the three individual orders is a posterior distribution of the global rate of activity  
429 pattern evolution, comparing the overall speed at which transitions between activity  
430 patterns have occurred along the branches of the phylogenetic tree during the course  
431 of each group's evolution. The global rates are estimated simultaneously with the  
432 patterns of pairwise transition rates – see STAR Methods for more details. See also  
433 Figure S1 for results from other mammal groups.

## 434 **STAR Methods**

### 435 **CONTACT FOR REAGENT AND RESOURCE SHARING**

436 Further information and requests for resources should be directed to and will be  
437 fulfilled by the Lead Contact, Chris Venditti ([c.d.venditti@reading.ac.uk](mailto:c.d.venditti@reading.ac.uk)).

### 438 **METHOD DETAILS**

#### 439 *The variable-rates regression model*

440 We used the variable-rates regression model [7, 13] to simultaneously estimate  
441 phylogenetic regression parameters whilst identifying the position and magnitude of  
442 rate shifts in the phylogenetically structured residual variance of the eye shape  
443 relationship (see below). The variable-rates model partitions the underlying Brownian  
444 variance ( $\sigma^2$ ) of a continuously varying generalized least squares model of trait  
445 evolution [e.g. 47] into two components: (1) a background rate ( $\sigma_b^2$ ) and (2) a set of  
446 rate scalars  $r$  defining branch-specific shifts. Note that this background rate  $\sigma_b^2$   
447 measures the instantaneous variance of change (i.e. change per unit time) acting  
448 along each individual branch of the phylogenetic tree. Together,  $\sigma_b^2$  and  $r$  estimate an  
449 optimized variance for each branch ( $\sigma_v^2 = \sigma_b^2 r$ ), and identify where branches have  
450 evolved faster ( $r > 1$ ) or slower ( $0 \leq r < 1$ ) than the background rate. A gamma prior  
451 ( $\alpha = 1.1$ ,  $\beta$  rescaled to give a median of 1) is placed on each scalar parameter, ensuring  
452 an even number of rate increases and rate decreases are proposed. Importantly,  
453 contrary to what has previously been reported [48] there is no prior placed on the  
454 number of rate parameters, i.e. the reversible-jump procedure flexibly allows for  
455 anywhere between 0 and  $n$  scalars to be estimated (where  $n$  is the number of nodes,  
456 including tips, in the phylogeny).

457 The presence of rate heterogeneity can be identified using Bayes factors ( $BF$ ),  
458 calculated as  $BF = -2 \log_e [m_1/m_0]$ , where  $m_0$  and  $m_1$  are the marginal likelihoods of  
459 a single-rate Brownian motion regression model and the variable-rates regression  
460 model respectively. Marginal likelihoods are estimated using a stepping stone sampler  
461 [49], where values are drawn from a beta-distribution ( $\alpha = 0.4$ ,  $\beta = 1$ ) [49]. Where  $BF$   
462  $> 2$  it is regarded positive support for rate variation [50].

463 The variable-rates regression model is implemented within a Bayesian Markov chain  
464 Monte Carlo (MCMC) reversible-jump framework and was introduced by Venditti *et al*  
465 (2011) [13] and Baker et al 2016 [7]. It is run using BayesTraits V3 (see below for link  
466 to software download).

#### 467 *The transition-rates model*

468 We estimated discrete transition rates (the rate of switching between different states  
469 along individual branches of a phylogenetic tree) among activity patterns using a  
470 Continuous-time Markov transition model implemented within a Bayesian framework  
471 [34, 35]. The model seeks to estimate the values of a transition matrix that define the  
472 instantaneous rate of switching between each pair of states (i.e. from nocturnal to  
473 diurnal, diurnal to nocturnal, etc.). The model we use is implemented in a reversible-  
474 jump framework which allows the dimensionality of the estimated transition rate matrix  
475 to be reduced where required to avoid over parameterization [35]. This allows two or  
476 more rates in the matrix to take the same value (if supported by the data) – or even  
477 for all rates to have different values. More details about the Markov transition model  
478 and its implementation in the reversible-jump framework can be found in Pagel and  
479 Meade (2006) [35].

480 We also implement a recently published variant of the Continuous-time Markov  
481 transition model [40] which allows for normalization of the estimated transition rate  
482 matrix. That is, the model simultaneously estimates the transition rates among states  
483 (as in the standard reversible-jump model [35]) alongside a *global rate* of evolution.  
484 The pattern of transition rates is still inferred, but the rate parameters are not directly  
485 interpretable. Instead, the global rate describes the overall speed at which transitions  
486 between states have occurred along the branches of the phylogenetic tree during the  
487 course of a group's evolution. That is, rates can be interpreted as deviations from a  
488 generalized rate acting across any set of data [40]. Therefore, estimating a global rate  
489 for the evolution of a single character among multiple different groups facilitates  
490 comparisons between the overall rates of change of a character regardless of the  
491 patterns of transition rates. Details of how the normalization constant is calculated can  
492 be found in Pagel & Meade, 2018 [40].

493 We use BayesTraits V3 [51] to run all discrete character transition models (see below).

## 494 **QUANTIFICATION AND STATISTICAL ANALYSIS**

### 495 *Modelling the eye shape relationship*

496 Mammal eye shape was described using the previously described relationship  
497 between corneal diameter and axial length [17, 26, 52] for  $n = 266$  species spanning  
498 29 mammalian orders (figure 1). All measurements were taken from Hall *et al*, 2012  
499 [17], matched to the recently published time tree of life [15], and  $\log_{10}$ -transformed.  
500 For the 266 species with eye shape data, we obtained activity patterns from the same  
501 source [17], where species are defined as nocturnal (typically active at night),  
502 cathemeral (active at both day and night), or diurnal (typically active at day). Sample

503 sizes for all models are recorded in the figure captions of the main text; all data and  
504 sources can be found in Table S3.

505 Significance of regression parameters was assessed by the proportion of the posterior  
506 distribution that crosses zero ( $P_x$ ). Where  $P_x < 0.05$ , that variable can be considered  
507 significantly different from zero. To compare parameters amongst different activity  
508 patterns, we compared the estimated slopes for each state using pairwise  
509 comparisons between the differences of two parameters at each iteration and  
510 assessed the proportion of the posterior distribution of differences crossing zero  
511 ( $P_{x[diff]}$ ). Where  $P_{x[diff]} < 0.05$ , two parameters are considered distinct. For our  
512 regression models, we summarize the median parameter values and their variance in  
513 Table S1, and visualize parameters and their differences in Figure 2.

514 All MCMC chains were run for a total of 200 million iterations, sampling every 100,000  
515 iterations after convergence and were repeated multiple times to ensure convergence.  
516 Uniform priors ranging between -10 and 10 were placed on all estimated regression  
517 coefficients. We ensured that the effective sample size for all estimated parameters  
518 was greater than 750, calculated using R package coda [53].

### 519 *Identifying rate shifts*

520 We defined significant *rate shifts* where there was significant unexplained residual  
521 variance away from an estimated underlying evolutionary relationship (see below for  
522 details of what relationships were studied). Where the posterior distribution of  
523 estimated  $r$  for a branch exceeded 1 in  $\geq 95\%$  of the posterior distribution, that branch  
524 was defined as a significant rate shift – it is evolving at a significantly faster rate to the  
525 background rate (note that rate decreases could also be identified where  $r < 1$  in 95%  
526 of the posterior). Although significance is identified across the posterior sample, we



527 summarize  $r$  for individual branches using modes (calculated using kernel density  
528 estimation across the posterior distribution) and for clades comprised of multiple  
529 branches, we report the range of branchwise modes of  $r$  (modal  $r$  range).

### 530 *Detecting the drivers of rate shifts*

531 We first identified rate shifts in eye shape evolution using a bivariate regression  
532 between corneal diameter and axial eye length (*simple eye shape model*). We then  
533 compared the subset of branches identified in this model to those identified as  
534 significant rate shifts in a model allowing for different slopes and intercepts in the  
535 relationship for each of the three activity patterns (*activity pattern model*). Note that  
536 these models estimate both regression parameters and rate scalars simultaneously.

537 Branches identified as rate shifts in the bivariate linear model represent significant  
538 unexplained variance in eye shape. If this unexplained variance can be explained by  
539 the differential slopes in the eye shape relationship faced by mammals of different  
540 activity patterns – i.e. differences in the slope of the relationship between corneal  
541 diameter and axial eye length as has previously been reported in birds [20] – we would  
542 observe a reduction in the number of identified branches in our activity pattern model  
543 (Figure S1). This is because activity pattern will explain the previously exceptional  
544 deviations away from the underlying eye shape relationship that manifested as bursts  
545 of rapid evolution by reducing the phylogenetically structured residual variance in eye  
546 shape; i.e. activity pattern explains the previously unexplained residual variance  
547 (Figure S1).

548 In the (unlikely) scenario in which activity pattern has not exerted sufficient selection  
549 pressure to change eye shape, then incorporating activity pattern into our tests for  
550 selection would result in no reduction in the number of branches identified as having

551 rapid bursts of eye shape change along them (Figure S1). This is because there would  
552 be no link between the rate of eye shape change and activity pattern: beyond the  
553 underlying regression relationship and the overall background rate of eye shape  
554 change across all mammals, activity pattern explains no additional variation. The only  
555 way to explain bursts of eye shape change without including additional possible  
556 explanatory factors into our model would be to increase the rate of evolution along  
557 branches leading to changes in eye shape; we would therefore continue to detect rapid  
558 evolutionary change in eye shape (Figure S1).

559 As with any regression framework, it is important to recognize that factors should be  
560 tested using a hypotheses-driven approach to avoid variation being explained by  
561 chance. Here, we have strong a priori reasons for using activity pattern as an  
562 explanatory factor (see Results & Discussion).

### 563 *Modelling activity pattern evolution*

564 In order to reconstruct the evolution of activity pattern, we estimated discrete transition  
565 rates of activity pattern evolution across all mammals (N = 3014, supplementing our  
566 original dataset [17] with activity pattern classifications from the literature [54, 55],  
567 Table S3). Crepuscular species, those that are active in twilight hours [55] are, on  
568 average, presumed to experience similar light levels to cathemeral species and so  
569 here we collapse these species into a single category as in previous classifications  
570 [54] and in order to match the three-state classification used in our main variable rates  
571 regression analyses.

572 To estimate transition rates among activity patterns, we use a Continuous-time Markov  
573 transition model allowing all transition rates to vary implemented within a Bayesian  
574 framework [35]. To investigate potential different patterns present across the mammal

575 tree of life, we also ran an additional model estimating transition rates separately for  
576 all large orders of mammals: carnivores (N = 236), primates (N = 301), rodents (N =  
577 1098, cetartiodactyls (N = 209), insectivores (N = 249), and lagomorphs (N = 79). We  
578 also analyse marsupials (N = 252) as a single group. Note that although bats are also  
579 one of the largest orders (N = 533 with activity pattern data), we do not estimate  
580 transition rates separately for this group owing to the fact that they are predominantly  
581 nocturnal with very few exceptions (Table S3).

582 We implemented all models in a reversible-jump framework [35], effectively reducing  
583 the dimensionality of the estimated transition rate matrix where required to avoid over  
584 parameterization. This allows two or more rates in the matrix to take the same value  
585 (if supported by the data). We used a hyper-prior approach [35] to reduce inherent  
586 uncertainty and biases in prior choice [35, 56]. We placed an exponential distribution  
587 as the prior on transition rates (seeding the mean from a uniform distribution ranging  
588 between 0 and 2) [56-58]. Alternative prior distributions produce qualitatively identical  
589 results. All chains were run for 10 million iterations, sampling every 10,000 iterations  
590 after convergence. We repeated the analysis with multiple MCMC chains to ensure  
591 convergence.

592 Finally, for the three largest individual mammalian groups we present in the main text,  
593 we additionally ran models that normalized the estimated transition rate matrix [40].  
594 This estimated a *global rate* of activity pattern evolution, describing the overall speed  
595 at which transitions between activity patterns have occurred along the branches of the  
596 phylogenetic tree making it possible to determine whether activity patterns were  
597 evolving at faster or slower rates in different groups regardless of their overall patterns  
598 of change.

## 599 **DATA AND SOFTWARE AVAILABILITY**

600 The full dataset of eye shape measurements and activity patterns used in our main  
601 analysis is already published and available in Hall *et al*, 2012 [17]. In Table S3, we  
602 provide this dataset where we have matched taxa names to the recently published  
603 time tree of life [15]. For our multi-state activity pattern analysis, we aimed to  
604 incorporate all available data for all mammals (N = 3,014). This additional data was  
605 obtained from published literature and all sources and data are documented in Table  
606 S3.

607 We use BayesTraits V3 [51] to implement the variable-rates regression models [7] and  
608 discrete transition rates analyses [35, 40]. The code for this program is open-source  
609 and is freely available to download from the following website:

610 <http://www.evolution.rdg.ac.uk/BayesTraitsV3.0.1/BayesTraitsV3.0.1.html>.

611 **Supplemental Item Titles and Legends**

612 **Table S3: Eye shape, activity pattern, and diet data for mammals. Related to**  
613 **STAR Methods.** All data used in our analyses is recorded here, along with its original  
614 published source.