

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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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 β 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).

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 (σ^2) of a continuously varying generalized least squares model of trait
445 evolution [e.g. 47] into two components: (1) a background rate (σ_b^2) and (2) a set of
446 rate scalars r defining branch-specific shifts. Note that this background rate σ_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, σ_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 ($\alpha = 1.1$, β 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.