



Original Article

Evolving through day and night: origin and diversification of activity pattern in modern primates

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Activity patterns have profound implications on primates' morphology, physiology, and behavior and have likely driven their diversification. The last common ancestor of extant primates has been traditionally considered nocturnal although this notion has been recently debated due to emerging contradictory evidence. Previous studies underestimated the role of cathemerality (i.e., the ability to remain active throughout a 24-h cycle) by simplifying primate activity to the diurnal–nocturnal dichotomy. We estimated the evolutionary trajectories of activity patterns in primates and investigated how these may have influenced their diversification rates. We used a comprehensive data set to test multiple evolutionary hypotheses, following a robust Bayesian framework by using 5000 calibrated phylogenetic trees to account for phylogenetic uncertainty. Our results support a nocturnal ancestor that has shifted to diurnality in the Simiiformes, has retained nocturnality in Lorisiformes and most Lemuriformes, and shifted to cathemerality in the ancestor of Lemuridae. The diversification of activity patterns in primates seems to have mainly arose by speciation rather than shifts between activity patterns, suggesting a low flexibility of diurnal and nocturnal patterns and the key importance of cathemeral activity as transitional state to shift between more specialized activity patterns. A cathemeral activity seems to appear well before diurnality in Malagasy lemurs, suggesting an ancient origin of this trait on the island and rejecting the hypothesis of a recent transition. The present research contributes to further disentangle the adaptive role of activity patterns in primate evolution.

Key words: activity pattern, cathemerality, diversification, evolution, Lemuriformes, primates.

INTRODUCTION

Earth rotation plays a major role in ecology and behavior of species by determining a number of rapid changes throughout the 24-h cycle. Life on earth has evolved to cope with these cyclic changes by partitioning and exploiting time as an ecological resource (Kronfeld-Schor and Dayan 2003). Birds and mammals present numerous examples of time-partitioning strategies, with the former being predominantly diurnal and the latter being predominantly nocturnal (Charles-Dominique 1975). The adaptive role of different activity patterns has thus received considerable attention by both chronobiologists and chronoecologists (Enright 1970; Halle and Stenseth 2000; Schibler et al. 2001). Yet the ultimate reasons for the observed pattern also

lie on species phylogenetic history that only recently reached a fine-grained resolution thanks to quantitative genetic information and the development of new statistical approaches. The analysis of patterns and mechanisms of activity pattern at macroevolutionary scale is thus essential to understand the importance of time partitioning for species diversification. Primates are an ideal model to study macroevolutionary trajectories of activity patterns because they represent a speciose group distributed in both hemispheres, show a variety of activity patterns, and phylogenetic reconstructions including most species are available. Thus, they provide an opportunity to analyze the reciprocal effects of activity pattern evolution and lineage diversification.

Today, most extant primates are either diurnal or nocturnal, whereas only a minority are considered cathemeral (Curtis and Rasmussen 2006). Cathemerality, better known as diel activity among mammalogists (Halle 2006), indicates a flexible pattern with significant bouts of activity in both diurnal and nocturnal

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phases (Tattersall 1987). This pattern can vary throughout the year and in different locations. Among primates, cathemerality has been reported in 4 genera of lemurs (*Eulemur*, *Lemur*, *Hapalemur*, and *Prolemur*) and 1 genus of platyrrhine (*Aotus*) (Curtis 2007; Fernandez-Duque et al. 2010; Donati et al. 2013). Because of the growing number of reports of primates active over the 24-h cycle in recent years, the ecological and evolutionary determinants of activity patterns in primates, compared with other mammals, have aroused considerable attention (Curtis and Rasmussen 2006; Donati and Borgognini-Tarli 2006). Diurnal and nocturnal primates evolved specific visual adaptations, which are well distinguished from other mammals (Kay and Kirk 2000; Kirk 2004, 2006; Hall et al. 2012). The degree of specialization of the visual system in Primates (Heesy and Ross 2001; Bearder et al. 2006) prevent them to shift their activity between the diurnal phase and the nocturnal phase. Interestingly, the eyes of cathemeral species show a mixture of diurnal and nocturnal traits (Kirk 2006; Hall et al. 2012), which allow them to operate in very different light conditions. Thus, cathemerality in primates has been the focus of several studies over the last decades (Tattersall 1987; Curtis and Rasmussen 2006; Curtis 2007; Donati et al. 2013) and has prompted an intense debate on its origin and evolution (van Schaik and Kappeler 1996; Kappeler and Erkert 2003; Curtis and Rasmussen 2006; Donati and Borgognini-Tarli 2006; Donati et al. 2013).

Some authors have argued that the co-occurrence of both diurnal and nocturnal species in previous primate communities suggests a considerable evolutionary flexibility in activity pattern (Ankel-Simons and Rasmussen 2008) and that diurnality and nocturnality may have evolved independently several times throughout primate evolutionary history (Tan et al. 2005; Williams et al. 2010; Griffin et al. 2012; Joffe et al. 2013). A secondary return to nocturnality is widely accepted for the genus *Aotus* (Martin 1990) but has also been suggested for *Avahi* (Müller and Thalmann 2000), *Tarsius*, *Lepilemur*, *Daubentonia*, and the Lorisiformes (Lorisidae + Galagidae) (Tan et al. 2005; Joffe et al. 2013). However, the information from the eye characteristics and phylogenetic inferences is contradictory and the number of transitions between activity patterns during the primates' radiation is still unknown (Heesy and Ross 2001, 2004; Tan et al. 2005; Ross et al. 2007; Ankel-Simons and Rasmussen 2008; Joffe et al. 2013; Melin et al. 2013; Veilleux et al. 2013).

Primates are thought to have originated from small, arboreal, insectivorous mammals, resembling modern tree shrews and possums (Bloch and Boyer 2002) between the Cretaceous and the Paleocene (~65–75 Ma) (Martin et al. 2007; Meredith et al. 2011). The last common ancestor of extant primates has long been considered nocturnal (Cartmill 1972, 1974, 1992; Charles-Dominique 1975; Allman 1977; Rasmussen 1990; Crompton 1995; Lemelin 1999; Ravosa et al. 2000) although this notion has recently been debated due to emerging contradictory evidence (Heesy and Ross 2001, 2004; Tan et al. 2005; Ross et al. 2007; Ankel-Simons and Rasmussen 2008; Joffe et al. 2013; Melin et al. 2013; Veilleux et al. 2013). Parsimony reconstructions based on activity pattern, chromatic vision, and opsin genes point to nocturnal-like species (Heesy and Ross 2001, 2004; Ross et al. 2007; but see Ankel-Simons and Rasmussen 2008*). In contrast, chromatic vision and opsin gene relaxation in living strepsirrhines species suggest a different picture where earliest primates may have been diurnal or cathemeral (Tan and Li 1999; Tan et al. 2005; Melin et al. 2013; but see Veilleux et al. 2013).

*These citations amended 18-03-15 to move the words 'but see' from before 'Heesy and Ross...' to before 'Ankel-Simons and Rasmussen...'.

Over the last decade, several pieces of evidence have prompted the idea that lemurids or even the whole Primates order may have had a cathemeral common ancestor. First, recent estimates of body mass in ancestral primates fall within the range of extant cathemeral and diurnal species (but see Gebo 2004; approximately >1000g; Soligo and Martin 2005). In fact, with the exception of *Daubentonia madagascariensis*, *Nycticebus javanicus*, *Nycticebus bengalensis*, *Otolemur crassicaudatus*, and *Otolemur garnetti*, all nocturnal primates weigh less than 1000g (Charles-Dominique 1975; Wright 1989). Second, looking at the fossil record, the Paleocene Plesiadapiformes (i.e., by many considered the earliest known stem primates) exhibit a relative orbit size that is smaller than in extant primates (Kay and Cartmill 1977). In addition, stem euprimates such as *Teilhardina asiatica* (Ni et al. 2004) and *Archicebus achilles* (Ni et al. 2013) show an orbit diameter within the range of current diurnal and cathemeral species, dating the appearance of diurnality and/or cathemerality to the earliest Eocene (54.8–55.8 Ma). Third, although many mammal species are labeled as either diurnal or nocturnal depending on their predominant phase of activity, there is a remarkable flexibility between individuals, locations, and seasons (Halle and Stenseth 2000; Curtis and Rasmussen 2006; Rafinetti 2008). In contrast, cathemerality seems to be an exception in primates where a strict diurnal–nocturnal dichotomy has been considered the rule (Curtis and Rasmussen 2006).

Species diversification rates result from the balance of speciation and extinction rates. Life-history traits may allow species to take advantage of new ecological opportunities (Losos 2010) as well as determine their vulnerability to different threats (Purvis et al. 2000; Cardillo et al. 2005). As a consequence, species traits play a fundamental role in diversification by both promoting speciation and affecting extinction risk (Maddison et al. 2007). Activity pattern strongly influences many aspects of primate behavioral ecology (Charles-Dominique 1975; Wright 1989) and thus likely leads to differential rates of diversification, as demonstrated both in primates and other groups of mammals for other ecological traits such as diet, social behavior, and species interactions (Gómez and Verdú 2012; Magnuson-Ford and Otto 2012; Price et al. 2012; Rojas et al. 2012).

Griffin et al. (2012) recently estimated ancestral activity patterns in Primates, finding support for a nocturnal ancestor. However, the reciprocal interaction between rates of trait evolution and diversification rates is critical to understand the evolution of any group and has been demonstrated as pervasive in many clades of the tree of life (Maddison et al. 2007; FitzJohn et al. 2009; Goldberg et al. 2011; Goldberg and Igić 2012). Therefore, it is critical to test for the relation between the evolution of diurnality, nocturnality, and cathemerality and the diversification of primates. Magnuson-Ford and Otto (2012) found an association between speciation rates and diurnality in primates; however, the authors reduced the diversity of activity patterns to the diurnal–nocturnal dichotomy. Given the adaptations that are associated with cathemerality, this trait likely yields different effects on extinction and speciation rates compared with diurnality and nocturnality.

Here, we estimated the evolutionary trajectories of activity patterns in primates and investigate how these may have influenced their rates of diversification. We tested multiple evolutionary hypotheses following a Bayesian framework and used a large number of phylogenetic trees to account for phylogenetic uncertainty (Pagel 1994).

Because of the evidence from fossil records (Kay and Cartmill 1977; Ni et al. 2004; Ni et al. 2013) and the estimated body size of

ancestral primates (Soligo and Martin 2005), as well as the flexibility in activity that characterizes nonprimate mammals (Halle and Stenseth 2000; Curtis and Rasmussen 2006; Rafinetti 2008), 1) we predict cathemerality to appear early in primate evolution and to be retained or secondarily acquired in particular ecological context. Also, 2) we predict activity patterns to be associated with diversification rates as suggested by the paramount role of activity patterns in primates ecology (Charles-Dominique 1975; Wright 1989; Fleagle 2013). Since cathemerality has been recently reported in lemurs previously considered diurnal (Donati et al. 2013)), we predict this trait to have had an early origin during primate evolution. Finally, because of the morphological specialization that characterizes diurnal and nocturnal primates (Kay and Kirk 2000; Kirk 2004, 2006; Hall et al. 2012), 4) we predict transition rates to be low between diurnal and nocturnal species but high from and to cathemeral species.

MATERIALS AND METHODS

Data collection

We collected activity data for 349 species of primates from PanTHERIA database (Jones et al. 2009) and its raw data files (<http://www.utheria.org/>; last accessed December 2012). We complemented this information by collecting data from additional sources (Rowe 1996; Nowak and Paradiso 1999; Curtis 2007; Redding et al. 2010; Donati et al. 2013; Myers et al. 2013). Activity patterns were categorized as diurnal (D), nocturnal (N), and cathemeral (C). The official definition of cathemerality, that is, “significant amount of activity, particularly feeding and travelling, occurring within both the light and dark portions of the 24-hour cycle” (Tattersall 1987), contains the problem of quantifying the term significant and it has little operational power when comparing animals sampled very differently and/or over different time windows. Thus, we decided to use a nonquantitative but more comparable operational definition by considering cathemeral a species when it was reported to perform nonoccasionally all main daily activities (particularly feeding and travelling) both during the day and at night. Additionally, Tattersall's definition (1987) recognizes that cathemerality may in some cases describe a seasonal rather than a year-round activity pattern. Thus, because of the intrinsic flexibility of this pattern, we included in the definition also species that are known to be cathemeral only in particular seasons or locations (e.g., Donati et al. 2009, 2013). On the contrary, we excluded occasional reports of activity during one or the other phase, often due to disturbance of nocturnal animals during the diurnal phase.

Phylogenetic trees for the order Primates were downloaded from 10kTrees Website (Arnold et al. 2010). These phylogenies are sampled from a Bayesian phylogenetic analysis of 11 mitochondrial and 6 nuclear loci. We downloaded 10 000 time-calibrated phylogenies and the 50% majority rule consensus tree. 10kTrees phylogenies (Version 3) contain 301 species of primates of which 299 were present in our data set. We adapted the database of activity patterns to the taxa from the phylogeny. Whenever we lacked information about the activity pattern of a subspecies, we assigned the pattern of the corresponding species.

Association between diversification and activity patterns

We used the multistate speciation and extinction (MuSSE) model to analyze the relation between the tempo of evolution of activity

pattern and the diversification rate on the evolutionary history of extant Primates. MuSSE (FitzJohn 2012) is a generalization of BiSSE (binary state speciation and extinction; Maddison et al. 2007), and both models are implemented in the R package diversitree (FitzJohn 2012). These are character-dependent diversification models, in which lineages follow a birth–death process, and speciation and extinction rates at any given time depend on the value of the trait at that time (Maddison et al. 2007; FitzJohn 2012). The algorithm simultaneously estimates 3 parameters related to speciation (λ_{diurnal} , $\lambda_{\text{nocturnal}}$, $\lambda_{\text{cathemeral}}$), 3 parameters related to extinction (μ_{diurnal} , $\mu_{\text{nocturnal}}$, $\mu_{\text{cathemeral}}$), and 6 parameters related to transition rates (q) between any pair of activity patterns.

The estimation of the parameters was first performed with maximum likelihood (ML) across a distribution of 5000 time-calibrated trees. These trees were randomly chosen from the 10 000 trees that we downloaded from 10kTrees. To examine the uncertainty in the parameter estimates, 2 independent analyses using Bayesian Markov Chain Monte Carlo methods were also performed on the consensus tree (we ran each chain for 10 000 steps and discarded the first 1000 steps as “burn-in”). For each tree, we tested 4 models: a full model (FM), where speciation, extinction, and transition rates vary independently in each of the 3 activity patterns, and 3 models in which speciation rates (equal speciation, ES), extinction rates (equal extinction, EE), or both (equal diversification, ED) were constrained to be the same across activity patterns. To test the robustness of our results to a potential variation of speciation rates through time, we implemented the same 4 models described above but assuming that speciation rates vary linearly through time, such that $\lambda(t) = \lambda_0 + bt$ (Rolland et al. 2014). The parameter λ_0 is the speciation rate at present and b controls the rate of change in speciation rate through time (t). Extinction rates and transition rates are assumed constant through time. We compared the 8 models using the second-order Akaike information criterion (AICc) and the Akaike weights (w) as the weight of evidence for each model given all the tested models (Burnham and Anderson 2002).

According to Davis et al. (2013), a sample of at least 200, ideally 300, species is necessary to achieve a high power in the performance of diversification analyses. In addition, each state of the trait analyzed should be represented in at least 10% of the species in the tree. In the phylogenies we downloaded, however, cathemeral species comprise 8% of the tips. Thus, to test for the robustness of our model to the unbalanced tip ratio, we performed a sensitivity analysis. Because we cannot increase cathemeral species in our sample, we decreased the number of diurnal species (the most represented category) thus increasing the proportion of cathemeral species, and we assessed how sensible the estimated rates are to the unbalanced tip ratio. For this, we randomly sampled and removed 24, 49, 74, 99, 124, and 149 diurnal species from our consensus tree, hence obtaining trees of 275, 250, 225, 200, 175, and 150 species and increasing the proportion of cathemeral species from 8% to 16%. We repeated this sampling 100 times and estimated speciation, extinction, and transition rates from the resulting subsampled trees.

RESULTS

The time-independent FM was the evolutionary model that fitted the data best according to the ML results (Table 1). This model indicates that the Most Recent Common Ancestor (MRCA) of primates was most likely nocturnal (posterior probability = 0.93), with lower probability of being cathemeral (0.07). Nocturnality was retained

Table 1
Models specifications and performance

| Time dependence | Model | k | Log L | w |
|-----------------|-------|-----|-----------|--------|
| Independent | FM | 12 | -881.8902 | 0.6024 |
| Independent | ES | 10 | -885.1430 | 0.2034 |
| Independent | EE | 10 | -885.9168 | 0.0959 |
| Independent | ED | 8 | -892.5514 | 0.0011 |
| Dependent | FM | 15 | -881.9023 | 0.0222 |
| Dependent | ES | 11 | -885.1434 | 0.0692 |
| Dependent | EE | 13 | -885.9118 | 0.0037 |
| Dependent | ED | 9 | -892.6115 | 0.0004 |

FM = full model; ES = equal speciation; EE = equal extinction; ED = equal diversification; k = number of parameters; Log L = log likelihood; w = Akaike weights.

in the MRCA of Haplorhini (0.93), whereas diurnality may have appeared in the MRCA of Simiiformes (Catarrhines + Platyrrhines; $D = 0.51$; $N = 0.29$; $C = 0.21$) but was more certainly present in the respective MRCAs of Catarrhines (0.93) and Platyrrhines (0.99). Within Platyrrhines, the MRCA of *Aotus* reversed to nocturnality, and later 3 *Aotus* species shifted to cathemerality. In strepsirrhines, most species retained nocturnality while *Propithecus* sp. became diurnal and the MRCA of Lemuridae shifted to cathemerality, with an independent origin of diurnality in *Varecia* (Figure 1).

Under the time-independent FM, speciation rates were high in cathemeral species (hereafter all rates are multiplied by 10^3 , and values represent median \pm interquartile range: $D = 217.0 \pm 36.4$; $N = 198.0 \pm 53.5$; $C = 563.0 \pm 274.0$), whereas extinction rates were higher in nocturnal and cathemeral species ($D = 75.9 \pm 60.3$; $N = 155.0 \pm 65.4$; $C = 562.0 \pm 304.0$). This resulted in higher diversification rates in diurnal species ($D = 142.0 \pm 33.9$; $N = 42.7 \pm 24.8$; $C = 2.3 \pm 78.2$) (Figure 2). The fastest rates of transition are found from nocturnal to cathemeral species (12.1 ± 11.2), followed by transition from cathemeral to diurnal species (7.5 ± 8.7) and nocturnal species (5.8 ± 9.7). Lower rates were found for the transition from nocturnal to diurnal species (1.7 ± 2.1) and from diurnal to nocturnal species (2.1 ± 2.3) (see Supplementary Table S1 for all estimated rates in the 4 models).

The sensitivity analysis shows that increasing the least represented category above 10% does not considerably change the results. The uncertainty around the estimated rates slightly increases as tree size decreases. However, even with a sample of 200 species and a proportion of cathemeral species of 12%, the pattern obtained for the values of the estimated coefficients is consistent with the pattern that was obtained with the full data set (Supplementary Figures S2 and S3).

DISCUSSION

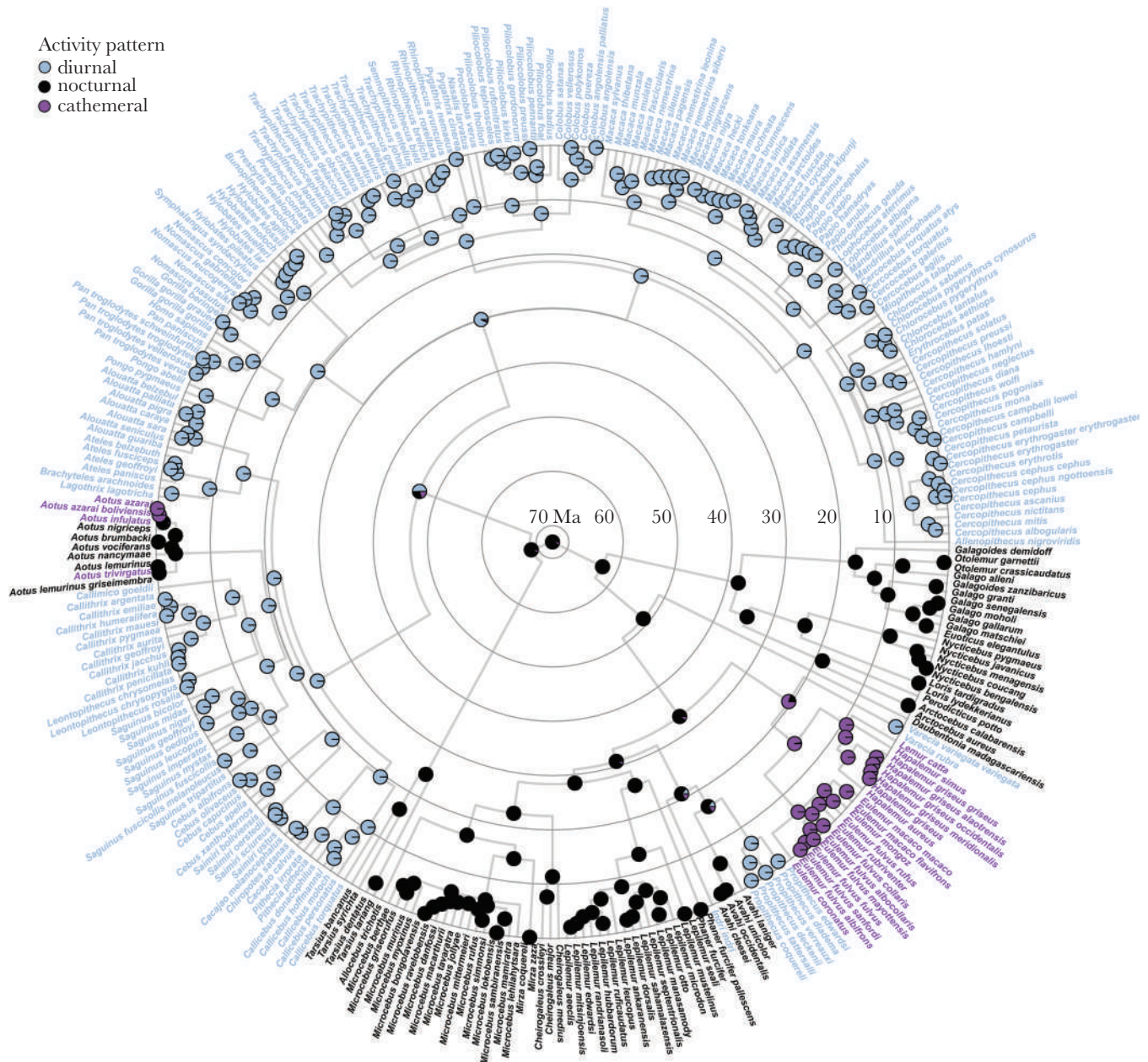
Ancestral activity patterns in Primates

This study provides the first approach to the reciprocal effects of a complex behavior (i.e., cathemerality) and lineage diversification in a group of vertebrates. Here, we characterized activity patterns by including also cathemerality, a trait that has evolved independently in many taxonomic orders of vertebrates (e.g., Charadriiformes, Anseriformes, Falconiformes, Cetartiodactyla, Carnivora, and Rodentia) but has been rarely considered in comparative analyses (Healy et al. 2015). Our results provide support for a nocturnal ancestor, in line with the traditional view of primate origins and supports previous parsimony analyses based on morphological,

physiological, behavioral, and paleontological data sets (Heesy and Ross 2001, 2004). In our model, Lorisiformes and the genera *Tarsius*, *Avahi*, *Lepilemur*, and *Daubentonia* retained nocturnality from primates MRCA and did not reverse to nocturnality from diurnal/cathemeral ancestors as suggested by some authors (Martin 1990; Müller and Thalmann 2000; Tan et al. 2005; Williams et al. 2010; Griffin et al. 2012; Joffe et al. 2013; Veilleux et al. 2013). Shifts in activity occurred in *Aotus* sp., first to nocturnality and secondarily to cathemerality in a few species, in *Propithecus* sp. to diurnality, and in the ancestor of Lemuridae to cathemerality. It has been suggested that *Aotus* might have shifted to nocturnality to avoid diurnal food competitors and predators (Wright 1989). Interestingly, *Aotus* species exhibit partial diurnal activity in areas that seem to be characterized by low predation and competition (Wright 1985). However, this adaptive explanation has been recently challenged because thermoregulatory aspects seem to play a more important role than the presence of predators/competitors in triggering diurnal activity of *Aotus* (Fernandez-Duque 2003; Fernandez-Duque and Erkert 2006). As a matter of fact, cathemeral *Aotus* are only found at the highest latitudes of the genus distribution, and equatorial species exhibit strict nocturnality (Khimji and Donati 2014). Beside the adaptive reasons for this activity shift, however, *Aotus* retained the ability to shift from a nocturnal to a diurnal life, as some traits of their visual adaptations in common with the cathemeral lemurs, for example, the absence of a *tapetum lucidum*, would also suggest (Kirk 2006). Thus, on a more speculative ground, species with mixed visual adaptations that we consider nocturnal might be cathemeral under certain conditions, which would imply in the case of *Aotus* only 1 main shift from diurnality to cathemerality. Within the Lemuridae, the genus *Varecia* may have shifted to diurnality although *Varecia* diurnal activity is still questionable as long-term studies on their nocturnal activity are lacking (Donati et al. 2013). Our estimation of ancestral states of activity pattern for the lemurs contrasts with previous findings where the MRCA was predicted to be diurnal and less likely cathemeral (Griffin et al. 2012). This mismatch may have arisen from differences in sample sizes, from the inclusion of the genus *Lemur* among cathemeral species (Donati et al. 2013), and because we tested a group of models that explicitly account for the reciprocal evolutionary interaction between activity pattern and lineage diversification. As previous analysis revealed (Ankel-Simons and Rasmussen 2008; Donati et al. 2013), this finding points out that cathemerality appeared early during the lemur radiation, around 20 Ma (Figure 1), and strongly rejects a scenario where this pattern was only recently acquired by lemurs as consequence of an ecological release (van Schaik and Kappeler 1996; Kappeler and Erkert 2003). Interestingly, our estimation also suggests that cathemerality actually preceded diurnality during the 60 million years of lemur evolution and most taxa did not shift to diurnality once this trait was acquired, thus highlighting the adaptive advantage that diel activity may have had over diurnality in the Madagascar island environment (Wright 1999; Curtis and Rasmussen 2006; Tattersall 2008; Donati et al. 2009, 2013).

Diversification of activity patterns in primates

Our results suggest that diversification rates in primates were constant through time although we cannot exclude that models with nonlinear time dependency could better explain the diversification of the clade. Our results also show that diurnal species diversify faster than nocturnal and cathemeral species because of their much lower extinction rate over time. We suggest 3 nonmutually exclusive hypotheses to explain this finding. First,

**Figure 1**

Estimated activity pattern at ancestral nodes of the consensus phylogeny under the FM. The pies at the nodes represent the posterior probabilities associated with each activity pattern. Diurnal = pale blue; nocturnal = black; cathemeral = purple.

the higher speciation rates in diurnal species may be related to the more frugivorous diet and the mutualistic relationships with plants compared with nocturnal primates (Lambert 2011). On average, seed dispersers have larger geographic ranges, possibly because they have expanded their own range in evolutionary times, and this may have indirectly promoted speciation and reduced extinction probability as found in previous phylogenetic comparative analyses (Gómez and Verdú 2012). Second, lower rates of diversification in nocturnal primates may be due to a higher competition with other nocturnal arboreal mammals (e.g., flying squirrels, sloths, procyonids, possums, and pteropodids), whereas heavier diurnal primates may have filled previously unoccupied niches (Charles-Dominique 1975). Although

this hypothesis has not been supported by any specific analysis so far, the available data indicate that most arboreal nonprimate mammals are nocturnal (Supplementary Figure S1). Third, a recent analysis strongly indicates that diurnal lifestyle have favored gregarious life (Shultz et al. 2011), probably to compensate for the increased predation risk associated with diurnal activity. Sociality may in turn have provided a number of advantages in terms of predator deterrence and mobbing, access to resources and mates, and protecting and rearing offspring (Fleagle 2013). In fact, sociality has been found to be associated with high speciation rates (Magnuson-Ford and Otto 2012), suggesting that diurnality may have indirectly prompted primate radiation.

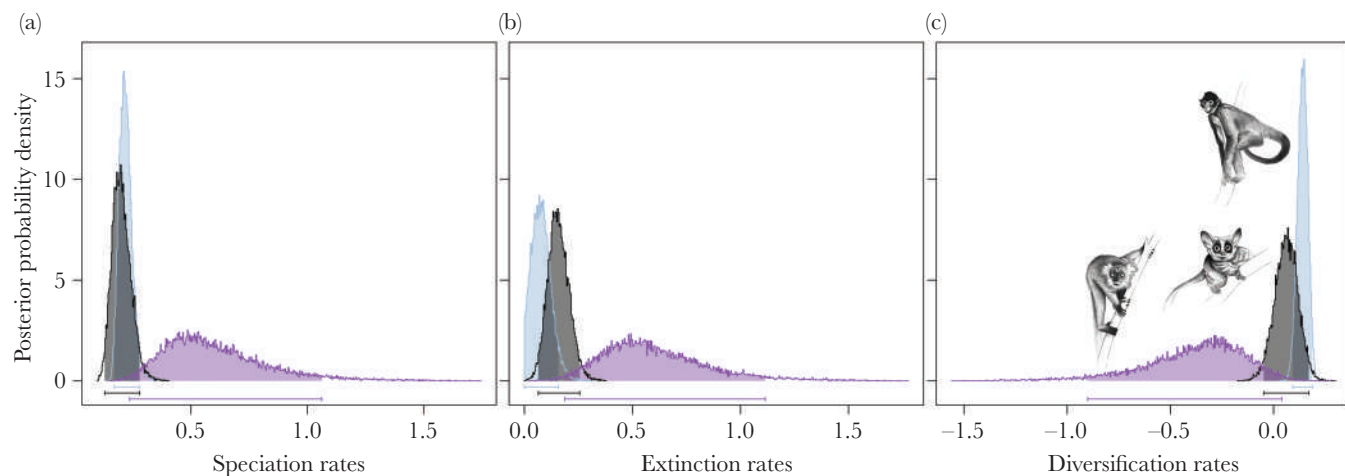


Figure 2

Speciation (a), extinction (b), and diversification rates (c) of diurnal (lighter color), nocturnal (darker color), and cathemeral (intermediate color) primates. The shaded areas correspond to the 95% credibility intervals of the posterior probability distributions. Drawings by Dawid Adam Iurino.

The model characterizes cathemeral species by high speciation and extinction rates. A more flexible pattern may have favored speciation allowing faster adaptation to new conditions of thermal stress, diet quality, and predation and competition intensity (Fernandez-Duque 2003; Curtis and Rasmussen 2006). Cathemeral animals, however, are potentially less competitive than more specialized species in stable environments and potentially more vulnerable to competitive exclusion (Futuyama and Moreno 1988; Kassen 2002). Intriguingly, our model suggests that cathemerality may have been the best strategy during transitional environmental conditions on the main continents and then be quickly replaced by more specialized, less flexible patterns. On the contrary, in less predictable environments, such as Madagascar, a cathemeral activity seems to have become a stable evolutionary strategy. Madagascar has a highly unpredictable environment characterized by extreme stochastic events (e.g., cyclones and storms), cyclical years of drought, and long and irregular phenological intervals compared with other tropical forests (Wright 1999; Bollen and Donati 2005; Dewar and Richard 2007). These environmental conditions have been used to explain many lemurid traits such as female dominance, monomorphism, low metabolic rates, and cathemeral activity as strategies to conserve energy (Wright 1999). It is then plausible that in Madagascar, optimal adaptive strategies for primates are different from those employed outside the island (Tattersall 1987; Curtis and Rasmussen 2006; Donati and Borgognini-Tarli 2006; Curtis 2007; Donati et al. 2013). Unfortunately, limitations due to sample size to perform robust phylogenetic analyses (Davis et al. 2013) do not allow to test Lemuriformes separately and we cannot exclude that in Madagascar, activity patterns have played a different role in the diversification of primates. Thus, until more fossil evidence will be collected and predictive morphometric measurements will be identified to estimate activity pattern in fossils, our interpretation remains on a speculative ground.

It has been argued that activity in primates has not severely constrained their evolution allowing transition from one state to another (Ankel-Simons and Rasmussen 2008) and shifts have probably happened several times (Joffe et al. 2013). However, transition rates in activity patterns are very low in our estimation, and the current diversity in activity pattern is mostly explained by diversification rates rather than shifts, suggesting a little potential for diurnal and nocturnal species to shift to the opposite activity pattern.

Activity shifts are in fact predicted to be rare events in primates if we consider the highly specialized visual adaptations in this group of mammals (Bearder et al. 2006; Kirk 2006). Moreover, it seems unlikely that the complex machinery of the endogenous circadian clock setup to opposite phases for a nocturnal or a diurnal animal may have shifted many times during primate evolution (Aschoff et al. 1982; Erkert and Cramer 2006). However, it is interesting to note that the highest shift velocity in our model are found in the transition from/to cathemerality, suggesting that cathemerality may have had a role as a transitional stage between more specialized activity patterns.

Caveats

As a note of caution, we must stress that the estimation of ancestral primates' activity only applies to the ancestors of extant primates and cannot be generalized to past primates' communities. Early primate communities may have included diurnal, nocturnal, and cathemeral species, coexisting by filling different available niches, as found in extant primate communities (Ankel-Simons and Rasmussen 2008). Also, our estimations rely on the known diversity of extant primates. Many likely diurnal Lemuriformes, for example, went extinct in historical times (van Schaik and Kappeler 1996; Kappeler and Erkert 2003) and thus they are missing from our sample. Finally, although in recent years there has been an increasing discovery of nocturnal species (Bearder 1999; Nekaris and Bearder 2007; Oliviera et al. 2007; Mittermeier et al. 2008; but see Yoder et al. 2000; Tattersall 2007), nocturnal primate diversity is probably underestimated because of the less evident morphological differences and the paucity of studies (Bearder 1999; Nekaris and Bearder 2007). However, the MuSSE analysis allows inferences to be made regarding the effect of a trait on diversification without complete phylogenetic information while still providing robust estimates (FitzJohn et al. 2009).

CONCLUSIONS

The present research contributes to further disentangle the adaptive role of activity patterns in primate evolution. Our Bayesian modeling over a large data set suggests that early primates were probably nocturnal and that diurnality, nocturnality, and cathemerality have been characterized by very different diversification

rates. The diversification of activity patterns in primates seems to have mainly arisen by speciation rather than shifts between activity patterns, suggesting a low flexibility of diurnal and nocturnal patterns but a key importance of cathemeral activity as transitional state between more specialized activity patterns. Cathemerality seems to have originated early during the lemur radiation where it has been fixed as a stable evolutionary strategy in the island unstable environment.

Time-partitioning strategies may have important implications in shaping the evolution and thus the behavior and ecology of species; further comparative analyses are needed to investigate the role of activity in the diversification of other taxa and to discern its effect from that of correlated traits.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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REFERENCES

- Allman J. 1977. Evolution of the visual system in early primates. *Prog Psychobiol Physiol Psychol.* 7:1–53.
- Ankel-Simons F, Rasmussen DT. 2008. Diurnality, nocturnality, and the evolution of primate visual systems. *Yearb Phys Anthropol.* 5:100–117.
- Arnold C, Matthews LJ, Nunn CL. 2010. The 10kTrees website: a new online resource for primate phylogeny. *Evol Anthropol.* 19:114–118.
- Aschoff J, Daan S, Groos GA. 1982. *Vertebrate circadian systems.* Berlin (Germany): Springer-Verlag.
- Bearder SK. 1999. Physical and social diversity among nocturnal primates: a new view based on long term research. *Primates.* 40:267–282.
- Bearder SK, Nekaris K, Curtis D. 2006. A re-evaluation of the role of vision in the activity and communication of nocturnal primates. *Folia Primatol.* 77:104–122.
- Bloch JI, Boyer DM. 2002. Grasping primate origins. *Science.* 298:1606–1610.
- Bollen A, Donati G. 2005. Phenology of the littoral forest of Sainte Luce, Southeastern Madagascar. *Biotropica.* 37:32–43.
- Burnham KP, Anderson DR. 2002. *Model selection and multimodel inference: a practical information-theoretic approach.* New York: Springer.
- Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds ORP, Sechrest W, Orme CDL, Purvis A. 2005. Multiple causes of high extinction risk in large mammal species. *Science.* 309:1239–1241.
- Cartmill M. 1972. Arboreal adaptations and the origin of the order Primates. In: Tuttle RH, editor. *The functional and evolutionary biology of primates.* Chicago (IL): Aldine-Atherton. p. 97–122.
- Cartmill M. 1974. Rethinking primate origins. *Science.* 184:436–443.
- Cartmill M. 1992. New views on primate origins. *Evol Anthropol.* 1:105–111.
- Charles-Dominique P. 1975. Nocturnality and diurnality: an ecological interpretation of these two modes of life by an analysis of the higher vertebrate fauna in tropical forest ecosystems. In: Luckett WP, Szalay FS, editors. *Phylogeny of the primates: a multidisciplinary approach.* New York: Plenum Press.
- Crompton RH. 1995. Visual predation, habitat structure, and the ancestral primate niche. In: Alterman L, Doyle GA, Izard MK, editors. *Creatures of the dark: the nocturnal prosimians.* New York: Plenum Press. p. 11–30.
- Curtis DJ. 2007. Cathemerality in lemurs. In: Gould L, Sauther ML, editors. *Lemurs: ecology and adaptation.* New York: Springer. p. 133–157.
- Curtis DJ, Donati G. 2013. Is temporal plasticity in lemurs a strategy for dealing with unpredictable or predictable, seasonal environments? In: Masters J, Gamba M, Génin F, editors. *Leaping ahead.* New York: Springer. p. 41–48.
- Curtis DJ, Rasmussen MA. 2006. The evolution of cathemerality in primates and other mammals: a comparative and chronoecological approach. *Folia Primatol.* 77:178–193.
- Davis MP, Midford PE, Maddison W. 2013. Exploring power and parameter estimation of the BiSSE method for analyzing species diversification. *BMC Evol Biol.* 13:38.
- Dewar R, Richard A. 2007. Evolution in the hypervariable environment of Madagascar. *Proc Natl Acad Sci USA.* 104:13723–13727.
- Donati G, Baldi N, Morelli V, Ganzhorn JU, Borgognini-Tarli S. 2009. Proximate and ultimate determinants of cathemeral activity in brown lemurs. *Anim Behav.* 77:317–325.
- Donati G, Borgognini-Tarli SM. 2006. From darkness to day-light: cathemeral activity in primates. *Am J Phys Anthropol.* 84:7–32.
- Donati G, Santini L, Razafindramana J, Boitani L, Borgognini-Tarli S. 2013. (Un-)Expected nocturnal activity in “diurnal” *Lemur catta* supports cathemerality as one of the key adaptations of the lemurid radiation. *Am J Phys Anthropol.* 150:99–106.
- Enright JT. 1970. Ecological aspects of endogenous rhythmicity. *Annu Rev Ecol Syst.* 1:221–238.
- Erkert HG, Cramer B. 2006. Chronobiological background to cathemerality: circadian rhythms in *Eulemur fulvus albifrons* (Prosimii) and *Aotus azarai boliviensis* (Anthropoidea). *Folia Primatol.* 77:87–103.
- Fernandez-Duque E. 2003. Influences of moonlight, ambient temperature, and food availability on the diurnal and nocturnal activity of owl monkeys (*Aotus azarai*). *Behav Ecol Sociobiol.* 54:359–369.
- Fernandez-Duque E, Erkert HG. 2006. Cathemerality and lunar periodicity of activity rhythms in owl monkeys of the Argentinian Chaco. *Folia Primatol.* 77:123–138.
- Fernandez-Duque E, de la Iglesia H, Erkert H. 2010. Moonstruck primates: owl monkeys (*Aotus*) need moonlight for nocturnal activity in their natural environment. *PLoS One.* 5:e12572.
- FitzJohn RG. 2012. Diversitree: comparative phylogenetic analyses of diversification in R. *Methods Ecol Evol.* 3:1084–1092.
- FitzJohn RG, Maddison WP, Otto SP. 2009. Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Syst Biol.* 58:595–611.
- Fleagle JG. 2013. *Primate adaptation and evolution.* 3rd ed. New York: Academic Press.
- Futuyama DJ, Moreno G. 1988. The evolution of ecological specialization. *Annu Rev Ecol Syst.* 19:207–233.
- Gebo DL. 2004. A shrew-sized origin for primates. *Yearb Phys Anthropol.* 47:40–62.
- Goldberg EE, Igić B. 2012. Tempo and mode in plant breeding system evolution. *Evolution.* 66:3701–3709.
- Goldberg EE, Lancaster LT, Ree RH. 2011. Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. *Syst Biol.* 60:451–465.
- Gómez JM, Verdú M. 2012. Mutualism with plants drives primate diversification. *Syst Biol.* 61:567–577.
- Griffin RH, Matthews IJ, Nunn CL. 2012. Evolutionary disequilibrium and activity period in primates: a Bayesian phylogenetic approach. *Am J Phys Anthropol.* 147:409–416.
- Hall MI, Kamilar JM, Kirk EC. 2012. Eye shape and the nocturnal bottleneck of mammals. *Proc R Soc B.* 279:4962–4968.
- Halle S. 2006. Polyphasic activity pattern in small mammals. *Folia Primatol.* 77:15–26.
- Halle S, Stenseth NC. 2000. *Activity patterns in small mammals: an ecological approach.* New York: Springer.
- Healy K, Guillerme T, Finlay S, Kane A, Kelly SBA, McClean D, Kelly DJ, Donohue I, Jackson AL, Cooper N. 2015. Ecology and mode-of-life explain lifespan variation in birds and mammals. *Proc R Soc B.* 282:20140298.
- Heesy CP, Ross CF. 2001. Evolution of activity patterns and chromatic vision in primates: morphometrics, genetics and cladistics. *J Hum Evol.* 40:111–149.
- Heesy CP, Ross CF. 2004. Mosaic evolution of activity pattern, diet and color vision in haplorhine primates. In: Kay CRR, editor. *Anthropoid origins: new visions.* New York: Kluwer Academic/Plenum Press. p. 665–698.

- Joffe B, Peichl L, Hendrickson A, Leonhardt H, Solovei I. 2013. Diurnality and nocturnality in primates: an analysis from the rod photoreceptor nuclei perspective. *Evol Biol*. doi: 10.1007/s11692-013-9240-9.
- Jones KE, Bielby J, Cardillo M, Fritz SA, O'Dell J, Orme CDL, Safi K, Sechrest W, Boakes EH, Carbone C. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*. 90:2648.
- Kappeler PM, Erkert HG. 2003. On the move around the clock: correlates and determinants of cathemeral activity in wild redfronted lemurs (*Eulemur fulvus rufus*). *Behav Ecol Sociobiol*. 54:359–369.
- Kassen R. 2002. The experimental evolution of specialists, generalists, and the maintenance of diversity. *J Evol Biol*. 15:173–190.
- Kay RF, Cartmill M. 1977. Cranial morphology and adaptation of Palaeochthon nacimienti and other Paromomyidae (Plesiadapoidea, Primates) with a description of a new genus and species. *J Hum Evol*. 6:19–53.
- Kay RF, Kirk EC. 2000. Osteological evidence for the evolution of activity pattern and visual acuity in primates. *Am J Phys Anthropol*. 113:235–262.
- Khimji SN, Donati G. 2014. Are rainforest owl monkeys cathemeral? Diurnal activity of black-headed owl monkeys, *Aotus nigriceps*, at Manu Biosphere Reserve, Peru. *Primates*. 55:19–24.
- Kirk EC. 2004. Comparative morphology of the eye in primates. *Anat Rec A Discov Mol Cell Evol Biol*. 281A:1095–1103.
- Kirk EC. 2006. Eye morphology in cathemeral lemurids and other mammals. *Folia Primatol*. 77:27–49.
- Kronfeld-Schor N, Dayan T. 2003. Partitioning of time as an ecological resource. *Annu Rev Ecol Evol Syst*. 34:152–181.
- Lambert JE. 2011. Primate seed dispersers as umbrella species: a case study from Kibale National Park, Uganda, with implications for Afrotropical forest conservation. *Am J Phys Anthropol*. 73:9–24.
- Lemelin P. 1999. Morphological correlates of substrate use in didelphid marsupials: implications for primate origins. *J Zool*. 247:165–175.
- Losos JB. 2010. Radiation, ecological opportunity, and evolutionary determinism. *Am Nat*. 175:623–639.
- Maddison W, Midford PE, Otto SP. 2007. Estimating a binary character's effect on speciation and extinction. *Syst Biol*. 56:701–710.
- Magnuson-Ford K, Otto SP. 2012. Linking the investigations of character evolution and species diversification. *Am Nat*. 180:225–245.
- Martin RD. 1990. Primate origins and evolution: a phylogenetic reconstruction. London: Princeton University Press.
- Martin RD, Soligo C, Tavaré S. 2007. Primate origins: implications of a Cretaceous ancestry. *Folia Primatol*. 78:277–296.
- Melin AD, Matsushita Y, Moritz GL, Dominy NJ, Kawamura S. 2013. Inferred L/M cone opsin polymorphism of ancestral tarsiers sheds dim light on the origin of anthropoid primates. *Proc R Soc B*. 280.
- Meredith RW, Janečka JE, Gatesy J, Ryder OA, Fisher CA, Teeling EC, Goodbla A, Eizirik E, Simão TLL, Stadler T, et al. 2011. Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science*. 334:521–524.
- Mittermeier RA, Ganzhorn JU, Konstant WR, Glander K, Tattersall I, Groves CP, Rylands AB, Hapke A, Ratsimbazafy J, Mayor MI. 2008. Lemur diversity in Madagascar. *Int J Primatol*. 29:1607–1656.
- Müller AE, Thalmann U. 2000. Origin and evolution of primate social organisation: a reconstruction. *Biol Rev*. 75:405–435.
- Myers P, Espinosa R, Parr CS, Jones T, Hammond GS, Dewey TA. 2013. The animal diversity web [cited 2012 August] Available from: <http://animaldiversity.org/>.
- Nekaris A, Bearder SK. 2007. The Lorisiform primates of Asia and Mainland Africa: diversity shrouded in darkness. In: Campbell CJ, Fuentes A, Mackinnon KC, Panger M, Bearder SK, editors. *Primates in perspective*. Oxford: Oxford University Press. p. 24–45.
- Ni X, Gebo DL, Dagosto M, Meng J, Tafforeau P, Flynn JJ, Beard KC. 2013. The oldest known primate skeleton and early haplorhine evolution. *Nature*. 498:60–64.
- Ni X, Wang Y, Hu Y, Li C. 2004. A euprimate skull from the early Eocene of China. *Nature*. 427:65–68.
- Nowak RM, Paradiso JL. 1999. Walker's mammals of the world. Vol. 1. Baltimore (MD): The Johns Hopkins University Press.
- Olivieria G, Zimmermann E, Randrianambinab B, Rasoloharijaonab S, Rakotondravonyb D, Guschanskia K, Radespiela U. 2007. The ever-increasing diversity in mouse lemurs: three new species in north and northwestern Madagascar. *Mol Phylogenet Evol*. 43:309–327.
- Pagel M. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc R Soc B*. 255:37–45.
- Price SA, Hopkins SSB, Smith KK, Roth VL. 2012. Tempo of trophic evolution and its impact on mammalian diversification. *Proc Natl Acad Sci USA*. 109:7008–7012.
- Purvis A, Gittleman JL, Cowlshaw G, Mace GM. 2000. Predicting extinction risk in declining species. *Proc R Soc B*. 267:1947–1952.
- Rafinetti R. 2008. The diversity of temporal niches in mammals. *Biol Rhythm Res*. 39:173–192.
- Rasmussen DT. 1990. Primate origins: lessons from a neotropical marsupial. *Am J Primatol*. 22:263–277.
- Ravosa MJ, Hylander WL, Noble VE, Johnson KR, Kowalski EM. 2000. Masticatory stress, orbital orientation and the evolution of the primate postorbital bar. *J Hum Evol*. 38:667–693.
- Redding DW, DeWolff CV, Mooers AO. 2010. Evolutionary distinctiveness, threat status, and ecological oddity in primates. *Conserv Biol*. 24:1052–1058.
- Rojas D, Vale Á, Ferrero V, Navarro L. 2012. The role of frugivory in the diversification of bats in the Neotropics. *J Biogeogr*. 39:1948–1960.
- Rolland J, Condamine FL, Jiguet F, Morlon H. 2014. Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biol*. 12:e1001775.
- Ross CF, Hall MI, Heesy CP. 2007. Were basal primates nocturnal? Evidence from eye and orbit shape. In: Ravosa M, Dagosta M, editors. *Primate origins: adaptations and evolution*. New York: Springer. p. 233–256.
- Rowe N. 1996. The pictorial guide to the living primates. New York: Pogonias Press.
- van Schaik CP, Kappeler PM. 1996. The social systems of gregarious lemurs: lack of convergence with anthropoids due to evolutionary disequilibrium? *Ethology*. 102:915–941.
- Schibler U, Ripperger JA, Brown SA. 2001. Chronobiology—reducing time. *Science*. 293:437–438.
- Shultz S, Opie C, Atkinson QD. 2011. Stepwise evolution of stable sociality in primates. *Nature*. 479:219–224.
- Soligo C, Martin RD. 2005. Adaptive origins of primates revisited. *J Hum Evol*. 50:414–430.
- Tan I, Yoder A, Yamashita N, Li W. 2005. Evidence from opsin genes rejects nocturnality in ancestral primates. *Proc Natl Acad Sci USA*. 102:14712–14716.
- Tan Y, Li W. 1999. Trichromatic vision in prosimians. *Nature*. 402:36.
- Tattersall I. 1987. Cathemeral activity in primates: a definition. *Folia Primatol*. 49:200–202.
- Tattersall I. 2007. Madagascar's lemurs: cryptic diversity or taxonomic inflation? *Evol Anthropol*. 16:12–23.
- Tattersall I. 2008. Avoiding commitment: cathemerality among primates. *Biol Rhythm Res*. 39:213–228.
- Veilleux CC, Louis EE Jr, Bolnick DA. 2013. Nocturnal light environments influence color vision and signatures of selection on the OPN1SW opsin gene in nocturnal lemurs. *Mol Biol Evol*. 30:1420–1437.
- Williams BA, Kay RF, Kirk EC. 2010. New perspectives on anthropoid origins. *Proc Natl Acad Sci USA*. 107:4797–4804.
- Wright PC. 1985. The costs and benefits of nocturnality for *Aotus trivirgatus*: (the night monkey). City University of New York. p. 630.
- Wright PC. 1989. The nocturnal primate niche in the New World. *J Hum Evol*. 18:635–658.
- Wright PC. 1999. Lemur traits and Madagascar ecology: coping with an island environment. *Am J Phys Anthropol*. 29:31–72.
- Yoder AD, Rasoloarison RD, Goodman SM, Irwin JA, Atsalis S, Ravosa MJ, Ganzhorn JU. 2000. Remarkable species diversity in Malagasy mouse lemurs (primates, Microcebus). *Proc Natl Acad Sci USA*. 97:11325–11330.