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Sleep patterns, daytime predation, and the evolution of diurnal sleep site selection in lorisiforms

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Abstract

Objectives:

Synthesize information on sleep patterns, sleep site use, and daytime predation at sleep sites in lorisiforms of Asia and Africa (10 genera, 36 species), and infer patterns of evolution of sleep site selection.

Materials and methods:

We conducted fieldwork in 12 African and six Asian countries, collecting data on sleep sites, timing of sleep and predation during daytime. We obtained additional information from literature and through correspondence. Using a phylogenetic approach, we established ancestral states of sleep site selection in lorisiforms and traced their evolution.

Results:

The ancestral lorisiform was a fur-clinger and used dense tangles and branches/forks as sleep sites. Use of tree holes and nests as sleep sites emerged ~22 Mya (range 17–26 Mya) in Africa, and use of bamboo emerged ~11 (7–14) Mya in Asia and later in Africa. Fur clinging and some sleep sites (e.g., tree holes, nests, but not bamboo or dense tangles) show strong phylogenetic signal. Nests are used by *Galagoides*, *Paragalago*, *Galago* and *Otolemur*; treeholes by *Galago*, *Paragalago*, *Sciurocheirus* and *Perodicticus*; tangles by *Nycticebus*, *Loris*, *Galagoides*, *Galago*, *Euoticus*, *Otolemur*, *Perodicticus* and *Arctocebus*; all but *Sciurocheirus* and *Otolemur* additionally sleep on branches/forks. Daytime predation may affect sleep site selection and sleep patterns in some species of *Nycticebus*, *Galago*, *Galagoides*, *Otolemur* and *Perodicticus*. Most lorisiforms enter their sleep sites around sunrise and leave around sunset; several are active during twilight or, briefly, during daytime.

Conclusion: Variations in sleep behavior, sleep patterns and vulnerability to daytime predation provide a window into the variation that was present in sleep in early primates. Overall, lorisiforms use the daytime for sleeping and no species can be classified as cathemeral or polycyclic.

Keywords:

Sleep sites, Social organization, Strepsirhine

1. Introduction

To understand broader evolutionary implications of sleep among primates, including sleep architecture, type of sleep, intraspecific variation in sleep, sleep duration, and the ecological pressures selecting for sleep and sleep site selection, a comparative approach is required (Elgar, Pagel, & Harvey, 1988; Lesku, Roth II, Amlaner, & Lima, 2006; Rattenborg, Martinez-Gonzalez, & Lesku, 2009). Sleep can comprise more than 50% of a primate's activity budget (Campbell & Tobler, 1984). Sleep can occur in single continuous bouts or take the form of fragmented sleep with periods of nonsleep and activity amidst otherwise continuous sleep bouts. Thus, knowledge of sleep site selection and sleep patterns can provide valuable insights into a species' ecology, social behavior, and habitat requirements (Anderson, 2000; Grow & Gursky-Doyen, 2010; Gursky, 2003; Mueller & Thalmann, 2000).Where primates choose to sleep is not only related to their body size, degree of arboreality, competition, and pressure from predation and/or parasites, but also to their activity pattern (Anderson, 2000; Eberle & Kappeler, 2004; Lock & Anderson, 2013; Tagg, Willie, Petre, & Haggis, 2013).

More than 50% of primate species are nocturnal, yet comparative information on the ecology of sleep is lacking for many nocturnal taxa, vital for constructing scenarios about the evolution of primate sleep (Capellini, Barton, McNamara, Preston, & Nunn, 2008). The use of sleep sites in primates varies substantially, ranging from the ground, rocky outcrops, tree branches/forks, dense clumps of herbs and lianas, sleep platforms, tree cavities and nests that are self-constructed or constructed by other species. Use of nests (either self-constructed or made in tree holes or hollows) and platforms as sleep sites is common among strepsirhines and great apes, and, presumably, the earliest humans (Bearder et al., 2003; Fultz, Brent, Breaux, & Grand, 2013; Sabater, Veá, & Serrallonga, 1997; Samson & Shumaker, 2015b), but are rarely used by other haplorhines. Samson and Nunn (2015) distinguished these assembled nests, on the basis that for larger primates, tree hollows would not be a viable sleeping option, and suggest that ancestral Paleocene and Eocene primates probably had galago-like fixed point nest use. Since most monkeys do not use nests, nest use must have evolved multiple times. To be able to infer potential sleep site patterns in early primates (i.e., the ones for which only morphological data are available), we also must examine how body size, forelimb to hindlimb ratio, and hand dexterity combine to assist living primates in their sleep site choices (Covert, 2002; Gebo & Dagosto, 2004).

To examine the question further, Kappeler (1998) reviewed several explanations for the use of nests and tree cavities amongst primates, especially among lemurs. Nests may serve as concealment against predators and/or provide thermoregulatory benefits to prevent heat loss, especially for small and solitary primates (Charles-Dominique &Martin, 1972). Kappeler (1998) also posited that nests and tree cavities particularly benefit species with neonates too altricial to cling to their mother's fur by allowing them to be placed in a safe location. Through phylogenetic analyses of multiple primate taxa, he concluded that the latter hypothesis received most support for nocturnal strepsirhines. Kappeler (1998) notably lacked any *in situ* study of Asian lorises [instead citing Rasmussen (1986) and Ehrlich & MacBride (1989)]. Regarding the paucity of field data on many primate taxa, he urged further research of wild primates to understand better the evolution of sleep site selection.

Five years after Kappeler's review, Bearder et al. (2003), focusing on the African lorisiforms, also noted the scarcity of data on sleep sites and sleep patterns even though such data are vital to understanding diversity within nocturnal primates. Most of Bearder et al.'s (2003) data were based on studies conducted in the latter part of the last century. The authors found similarities among species within the same genus, but clear differences among genera.

In the twenty-first century, substantial taxonomic changes have occurred for both African and Asian lorisiforms. First, the dwarf galagos of the genus *Galagoides* were recognized as a polyphyletic clade (Pozziet al., 2015), and now are comprised of *Galagoides* (western and central Africa) and *Paragalago* (eastern Africa). *Paragalago* is a sister taxon to the genus *Galago* and *Galagoides* and is a sister taxon to the clade containing *Sciurocheirus*, *Otolemur*, *Paragalago* and *Galago* (Masters et al.,2017). Second, divergence among lorisiforms is estimated to be far more ancient than previously thought; for instance *Euoticus* split from other galagos ~30 Mya and *Arctocebus* split from *Perodicticus* ~23 Mya (Pozzi et al., 2015). Third, and related to the previous two points, more species are recognized (i.e. two additional species of *Perodicticus*, four *Nycticebus*, one *Galagoides*, and one *Sciurocheirus*). Fourth, researchers studying nocturnal primates have amassed substantial new field data from countries such as Angola, Cameroon, Equatorial Guinea, The Gambia, Kenya, Malawi, South Africa, Tanzania, Cambodia, India, Indonesia, Sri Lanka, and Vietnam (Bersacola, Svensson, & Bearder, 2015; Butynski & De Jong, 2004, 2007, 2017; Butynski, De Jong, Perkin, Bearder, & Honess, 2006; De Jong & Butynski, 2009; Engelbrecht, 2016; Génin et al., 2016; Kappeler et al., 2017; Kenyon et al., 2014; Kumara, Sasi, Chandran, & Radhakrishna, 2016; Nekaris, 2003a, b, 2014; Nekaris & Jayewardene, 2003; Pimley, Bearder, & Dixson, 2005a, b; Ray, Wren, & Bowers, 2016; Svensson & Bearder, 2013). Fifth, primatologists working on diurnal primates have taken an interesti n certain lorisiforms, as lorisiforms share sleep sites with diurnal primates (Llorente, Sabater, & Houle, 2003), or are hunted by them (Boesch & Boesch, 1989; Hardus et al., 2012; Nishida, Uehara, & Nyundo, 1979; O'Malley, 2010; Pruetz & Bertolani, 2007).

Combined, the recent advancements in our understanding of lorisiforms allow for an overview of sleep sites, sleep patterns, sleep associations, and predation pressure faced by lorisiforms while sleeping. Using new genetic data on the relationships within Lorisiformes, we predict when various sleeping patterns emerged within this group. The deep evolutionary divergence times between various lorisiform genera help us explicitly to address several questions. Do lorisiforms provide evidence that the early primate ancestors were fixed point nest users? Did nest using evolve multiple times amongst the lorisiforms? Does the ability of a neonate to cling to the mother's fur relate to the use of fixed point nests? These data can be used as a basis to understanding ancestral sleep behavior of primates that can help to inform sleep patterns that occurred later in primate evolution.

2. Material and methods

We follow the taxonomy of Nekaris (2013a,b), but recognize the genus *Paragalago* (Masters et al., 2017), *Nycticebus kayan*, *N. bancanus* and *N.borneanus* (Munds, Nekaris, & Ford, 2013), *Sciurocheirus makandensis* (Ambrose, 2013), and *Galagoides kumbirensis* (Svensson et al., 2017). We treat the Mount Kenya potto (*Perodicticus ibeanus stockleyi*) as a subspecies of *P. ibeanus*, not *P. potto* (Butynski & De Jong, 2017). As such, we include 10 genera with 36 species of lorisiform. In the subsequent text, we abbreviate *Galagoides* as *Gd*. to distinguish it from *Galago* (*G*.), and *Paragalago* as *Pg*. to distinguish it from *Perodicticus* (*P*.).

2.1 Data collection

Post-2003 (i.e., after the publication of Bearder et al.'s 2003 compendium) we conducted nocturnal field work in Angola (SKB, MSS; 1 mo), Cameroon (AML, TMB, YdJ; 3 mo), Democratic Republic of the Congo (TMB; 2 mo), Equatorial Guinea (Bioko: TMB; 12 mo), Ethiopia (TMB; 1mo), The Gambia (SKB, MSS; 1 mo), Kenya (TMB, YdJ; 34 mo), Nigeria (AL; 2 mo), Malawi (SKB; 1 mo), Rwanda (SKB, MSS; 1 mo), Tanzania (TMB, YdJ, CB, AP; 19 mo), Uganda (TMB, YdJ, MSS, AML; 19 mo), Cambodia (CRS, KAIN; 11 mo), India (KAIN, ND; 32 mo), Indonesia (Java: KAIN, VN, KDR, DS; 60 mo; Sumatra: KAIN; 1 mo), Malaysia (Borneo: DJS; 60 mo), Sri Lanka (KAIN, EP; 22 mo) and Vietnam (SAP,KAIN; 9 mo). We collected most data on populations where individuals could not be individually recognized, but in Borneo, Cambodia, India, Sri Lanka, Vietnam and Java, we followed identified individuals with radio collars or other markers. We obtained additional data from published studies and through correspondence with researchers, including those working on great apes (bonobos *Pan paniscus*, common chimpanzees *P. troglodytes*, Sumatran orangutan *Pongo abelii*, Bornean orangutan *P. pygmaeus* and Tapanuli orangutan *P. tapanuliensis*: Nater et al., 2017) to obtain data on predation events.

2.2 Analyses

We used species as the unit of analysis. We pooled data from studies to provide a global picture. Based on previous research (Bearder et al., 2003), we placed sleep site types into five groups: nests, tree holes or hollows, dense tangles of vegetation, tree branches/forks, and bamboo thickets. We ranked the use of sleep sites types from zero (no evidence of use), one (occasional use or mixed evidence) or two (regular use).

To typify social cohesion, we collected data on sleep group size. When transporting infants, these can be carried in the parent's mouth or they can cling on to their parent's fur. For each species we recorded whether they carried infants in the parent's mouth or if they can cling to their parent's fur, or whether they employed both methods. Regarding vocalizations, we included call types (audible to humans) used for social cohesion, advertisement and maintenance. We exclude the ultrasonic calls of P*erodicticus*, *Loris* and *Nycticebus*. We ranked vocalizations as one (social cohesion vocalizations displayed at sleep site) or zero (social cohesion vocalizations not displayed at sleep site). Intermembral Index (IMI, a ratio of forelimb length to hindlimb length) for the different species was taken from Fleagle (2013) and for slow and slender lorises from measurements taken by KAIN and DJS on wild-caught live animals.

To gain insight into sleep patterns and the presence of fragmented sleep in the lorisiforms, we compiled data on when individuals entered and exited sleep sites. From selected sites, we added information on pre-or post-dusk waking and pre- or post-dawn sleeping. We added observations of sleep during the night or non-sleep behavior during the day.

We examined evidence of predation on lorisiforms and highlight those instances where the events occurred while the animal was asleep, or where we could reasonably infer that predation had taken place during the daytime. We excluded predation events by nocturnal predators such as owls but included events from cathemeral or crepuscular predators. While we acknowledge that most lorisiforms, at least occasionally, sleep for brief periods during the night, and that they may be subject to predation by nocturnal predators at these times, this form of rest is distinctly different from them selecting and using a sleep site where they will sleep during day time. Additionally, we compiled information on anti-predator strategies used by lorisiforms and which of these might be most effective at sleep sites.

We carried out reconstruction of ancestral states on a subset of species for which full sleep site and fur clinging behavior and published genetic sequences were available. We obtained cytochrome *b* sequences (1,140 bp in length) of 23 species of lorisiform from GenBank (for accession numbers see Figure 1) and we aligned them with MAFFT v.7 multiple sequence alignment (Katoh & Standley, 2013). This formed the basis of our ancestral state reconstruction analyses. We constructed phylogenetic trees using BEAST v.2.4.6 (Bouckaert et al., 2014; Drummond & Rambaut, 2007; Suchard & Rambaut, 2009). We implemented a strict clock with the birth-death speciation tree prior for 100 million generations, sampling every 10,000 iterations. We checked analyses for convergence using Tracer v.1.6. We then used the posterior probability tree produced by BEAST to perform stochastic character mapping (Huelsenbeck, Nielsen, & Bollback, 2003) to infer ancestral states of sleep site and fur clinging using the R package phytools v.0.6–20 (Revell, 2012). Phylogenetic signal was tested for discrete character evolution of each character by comparing AICc scores with and without phylogenetic error structure using the fitDiscrete function in the R package, geiger v.2.0.6

(Harmon, Weir, Brock, Glor, & Challenger,2008). This signal was estimated by testing a model with complete phylogenetic independence (lambda fixed to 0) to one with phylogenetic nonindependence (free lambda tree transformation).

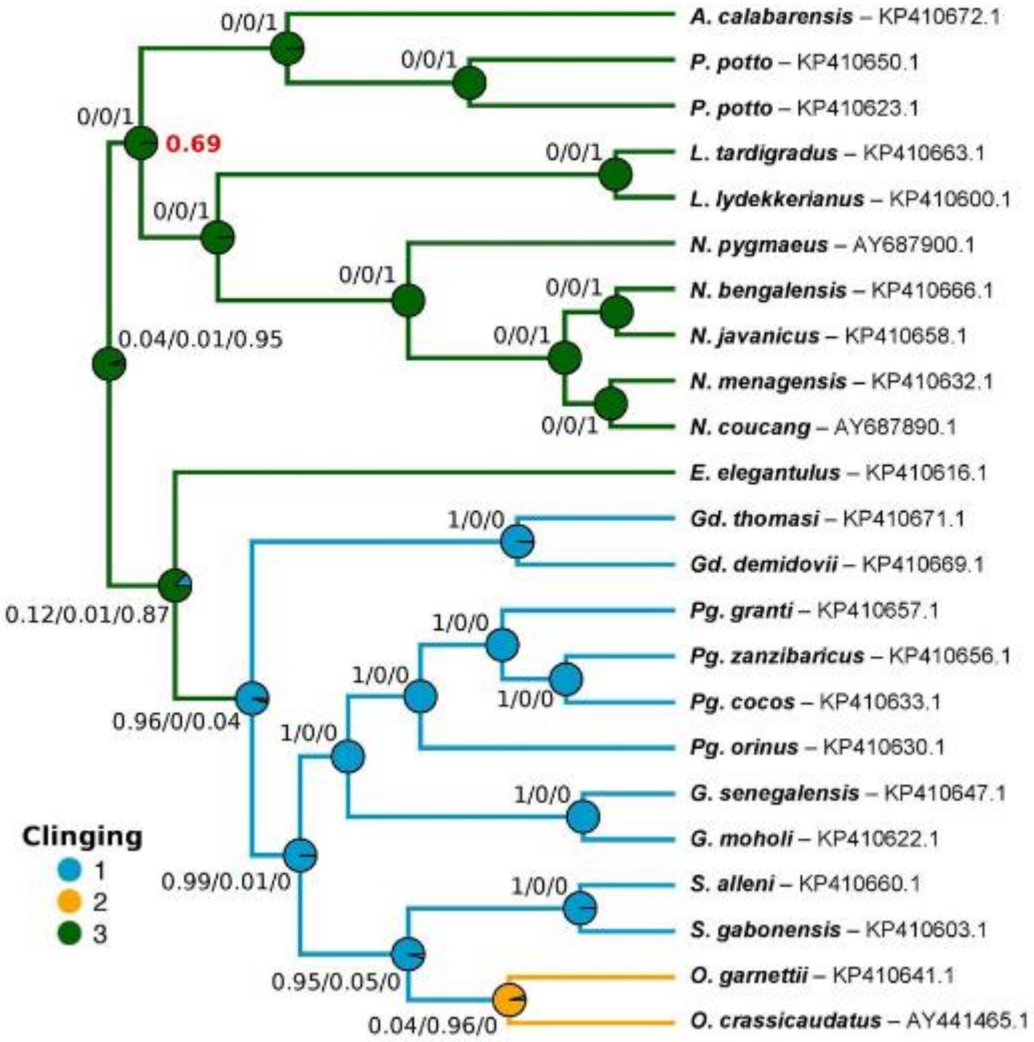

Figure 1 Ancestral state reconstructions of stochastic character mapping of lorisiform fur-clinging whereby infants cling onto the fur of their parents or group member when being transported. Red numbers indicate the Bayesian posterior probabilities of the phylogenetic tree if <1. Branches above nodes (closer to tips) are colored based on their ancestral state probability. Pie charts on nodes and black numbers (states 1/2/3) indicate the probability of the state in the common ancestor. The states are in the following order: 1 – absent, 2 – occasionally present, 3 – present.

We fitted stochastic character histories for each character set by executing continuous-time reversible Markov models, to sleep sites and fur clinging, over 99,900 simulations each. We used an equal rates of transition model to sample the state transition matrix “Q” from the posterior probability. We used ancestral character estimation (“ace”) to demonstrate the probabilities of states at each node. To date the timing of the ancestral states of sleep site and fur clinging, we used the timed phylogeny of Pozzi et al. (2015) to calculate mean values and 95% highest probability estimates in millions of years ago (Mya).

3. Results

3.1 Physical characteristics of sleep sites and evolution of sleep site selection

The type of sleep site lorisiforms most commonly used was tangles (67% or 24 of 36 species), followed by holes (44%, 16 species), branches/forks (44%, 16 species), nests (either self-built or built by other species: 33%, 12 species) and bamboo (14%, 5 species) (Table 1). Of the 24 species that use tangles, 62% also use branches/forks, 46% also use holes, and 42% also use nests. Of the 16 species that use branches/forks, 94% also use tangles. Of the 16 species that use holes, 69% also use nests, 69% also use tangles, and 31% also use branches/forks. Twelve species use nests, 92% of which also use holes and 83% also use tangles. Of the five species that use bamboo, the four Asian lorises also use branches/forks and tangles, but none use nests or holes, whilst *Gd. demidovii* mainly uses nests in dense undergrowth, and, to some extent, tree holes and tangles. Species in which infants cling to the adult's fur do not tend to use nests or tree holes.

The IMI ranges from lows of around 50 in *Galago* spp., representing clear vertical clingers and leapers with legs twice as long as their arms, to an intermediate value of around 70 in *Otolemur* and *Galagoides*, and highs of over 90 in *Loris* and *Nycticebus*, with arms and legs being almost the same length. Species with low IMIs tend to be those that carry their young in their mouth, and that use nests and tree holes, whereas species with intermediate IMIs tend to have infants that cling on the adult's fur and do not use nests or tree holes (Table 1).

At least four lorisiforms use human-made sleep sites. *Galago senegalensis* sleeps in traditional bee-hives (hollowed tree boles), bird-houses, and roofs of buildings while *G. moholi* uses ventilation pipes at some study sites. *Otolemur crassicaudatus* sleeps in traditional bee-hives and roofs of buildings, and *Pg. cocos* is also known to utilize human-made sleep sites.

Phylogenetic relationships showed strong support for all splits except for the sister group relationship between *Artocebus* + *Perodicticus* and *Nycticebus* + *Loris* (bpp = 50.63) (Figures 1 and 2). Fur clinging and some sleep sites show strong phylogenetic signal under a lambda transformation model: fur clinging (estimated lambda = 1, AICc = 25.175) is a better fit (ΔAICc = 22.08) than a model with no phylogenetic signal (lambda fixed to 0, AICc = 47.255); tree hole (estimated lambda = 1, AICc = 33.64) is a better fit (ΔAICc = 19.10) than a model with no phylogenetic signal (lambda fixed to 0, AICc = 52.74); branches/forks (estimated lambda = 0.98, AICc = 28.96) is a better fit (ΔAICc = 2.948) than a model with no phylogenetic signal (lambda fixed to 0, AICc = 31.91). Nests showed some support for phylogenetic signal (estimated lambda = 0.557, AICc = 47.01) and is a better fit (ΔAICc = 0.744) than a model with no phylogenetic signal (lambda fixed to 0, AICc = 47.75). Two sleep sites showed no support of phylogenetic signal: bamboo (estimated lambda = 0.363, AICc = 35.559) is a worse fit (ΔAICc = 20.144) than a model with no phylogenetic signal (lambda fixed to 0, AICc = 35.415); dense tangle (estimated lambda = 0.607, AICc = 44.78) is a worse fit (ΔAICc = 21.462) than a model with no phylogenetic signal (lambda fixed to 0, AICc = 43.318). Although stochastic character histories were estimated for all datasets, no information about ancestral evolution should be drawn

Table 1 Sleep site type

				Sleep site type					Social cohesion						
Species	Intermembral Index	Mouth-carrying	Fur-clinging	Nest	Tree hole	Dense tangle	Branch/fork	Bamboo	Audible advertising calls	Audible contact maintenance calls	Allogrooming at sleep site	Sleep group size (range)	Non-human diurnal and crepuscular predators (confirmed records in bold)	Predator avoidance strategies	Reference
Galagoides demidovii	68	2	0	2	1	1	0	1	1	1	?	2-10	**Sooty mangabeys, bonobos**		1; 2; 3; 4; 5; 6
Gd. thomasi	67	2	0	1	1	1	1	0	1	1	?	<5	Snakes, hawks, hornbill, viverrids, mongooses, **blue monkey**		7; 8; 9
Gd. kumbirensis		?	?	?	?	?	?	?	?	?	?	?	?		10
Paragalago orinus		1	0	2	1	1	?	0	1	?	1-5	1-9	Snakes, raptors, genets, Sykes's monkeys		11; 12; 13
Pg. rondoensis		2	0	2	0	?	?	?	1	0	?	<3	Snakes eg. forest cobras, boomslangs, green mambas		13
Pg. granti		2	0	2	2	0	0	0	1	0	?	4-5	Snakes eg. forest cobras, boomslangs, green mambas		13; 14; 15
Pg. cocos		2	0	0	2*	0	0	0	1	1	?	1-5	Snakes eg. forest cobras, boomslangs, green mambas, *Cercopithecus* monkeys		16; 17
Pg. zanzibaricus	60	2	0	2	2	2	0	0	1	1	?	1-5	Snakes eg. forest cobras, boomslangs, green mambas		13; 16; 17; 18
Galago senegalensis	52	2	0	1	2*	2	1	0	1	1	1	<6	**Chimpanzees**		19; 20; 21; 22; 23; 24; 25; 26; 27; 28; 29; 30

				Sleep site type					Social cohesion						
Species	**Intermembral Index**	**Mouth-carrying**	**Fur-clinging**	**Nest**	**Tree hole**	**Dense tangle**	**Branch/fork**	**Bamboo**	**Audible advertising calls**	**Audible contact maintenance calls**	**Allogrooming at sleep site**	**Sleep group size (range)**	**Non-human diurnal and crepuscular predators (confirmed records in bold)**	**Predator avoidance strategies**	**Reference**
G. gallarum		?	0	1	1	2	2	0	1	?	1	≤3	Snakes, raptors, jackals, mongooses, genets, wild cats	Live in the thorniest habitats of all galagos. Sleep and rest in the core of thorny vegetation.	17; 31; 32; 33; 34; 35
G. moholi	54	2	0	2	2*	1	1	0	1	0	?	1-8	Large snakes & monitor lizards, **genets**, **Verreaux's eagle**, small carnivores		13; 36; 37; 38; 39; 40; 41
G. matschiei		2	0	?	2	?	?	?	1	0	?	?	Large snakes, viverrids, **blue monkeys**, baboons, chimpanzees		7; 42
Sciurocheirus alleni	65	2	0	1	2	2	1	?	1	1	1	1-6	Large snake, viverrids		1; 16; 43; 44
S. gabonensis		2	0	0	2	?	0	?	1	?	?	1-3	Large snakes, viverrids, leopard, African golden cat		16; 45
S. cameronensis		2	0	1	2	?	?	?	?	?	?	1-6			16; 44; 46
S. makandensis		?	0	?	?	?	?	?	1	1	?	1-4	Large snakes, viverrids, golden cats		47; 48
Euoticus elegantulus	64	0	2	0	0	1?	1?	0	1	1	?	3-4	Pythons, viverrids		1; 13; 16
E. pallidus		0	2	0	2	0	1	0	1	1	?	1-4	Central African linsang		13; 16; 49
Otolemur crassicaudatus	70	1	1	1	1*	2	0	?	1	0	?	1-4	Large snakes, raptors, leopards, chimpanzees		13; 16; 17; 50

				Sleep site type					Social cohesion						
Species	**Intermembral Index**	**Mouth-carrying**	**Fur-clinging**	**Nest**	**Tree hole**	**Dense tangle**	**Branch/fork**	**Bamboo**	**Audible advertising calls**	**Audible contact maintenance calls**	**Allogrooming at sleep site**	**Sleep group size (range)**	**Non-human diurnal and crepuscular predators (confirmed records in bold)**	**Predator avoidance strategies**	**Reference**
O. garnettii	69	1	1	0	1	2	?	?	1	1	?	1-4	Large snakes, raptors		17; 51; 52; 53
Arctocebus calabarensis	89	0	2	0	0	2	1	0	0	0	?	1-2	Snakes, viverrids, monkeys		13
A. aureus		0	2	0	0	2	1	0	0	0	?	1-2	Large snakes, viverrids		13
Perodicticus potto	88	0	2	0	0	2	1	0	0	0	?	?	Large snakes, **African crowned eagles**, civets, black-legged mongoose, **leopards**, African golden cats, *Cercopithecus* monkeys, mandrills, **chimpanzees**	Scapular neck shield, predator defense posture, drops to ground	6; 19; 54; 55; 56; 57
P. edwardsi		0	2	0	?	2	?	0	0	0	?	1-2		Scapular neck shield, predator defense posture, drops to ground	43; 58; 59
P. ibeanus		0	2	?	?	2	?	0	0	0	?	?	**Leopard**	Scapular neck shield, predator defense posture, drops to ground	54; 5
Nycticebus javanicus	93	0	2	0	0	2	1	2	0	0	1	4		Venomous, predator defense posture	60
N. bengalensis		0	2	0	0	2	1	2	0	0	1	?		Venomous, sleeps high in trees inaccessible positions or in dense thorny tangles	61

				Sleep site type					Social cohesion						
Species	Intermembral Index	Mouth-carrying	Fur-clinging	Nest	Tree hole	Dense tangle	Branch/fork	Bamboo	Audible advertising calls	Audible contact maintenance calls	Allogrooming at sleep site	Sleep group size (range)	Non-human diurnal and crepuscular predators (confirmed records in bold)	Predator avoidance strategies	Reference
N. menagensis	91	0	2	0	0	2	1	0	0	0	1	1-3	**Reticulated pythons**, raptors	Venomous, predator defense posture	62
N. pygmaeus	91	0	2	0	0	2	1	1	1	1	1	1-5	Monitor lizards, raptor, small carnivores	Venomous, predator defense posture	63; 64
N. coucang	91	0	2	0	0	2	1	1	0	1	1	3	**Reticulated python, monitor lizards**	Venomous, predator defense posture	65; 66
N. hilleri	89	0	2	0	0	2	1	1	1	1	?	?	Changeable hawk eagle, **Sumatran orangutans**	Venomous, predator defense posture	67; 68; 69; 70
N. kayan		?	?	?	?	?	?	?	?	?	?	?		Venomous, predator defense posture	
N. bancanus		?	?	?	?	?	?	?	?	?	?	?	?	?	
N. borneanus		?	?	?	?	?	?	?	?	?	?	?	?	Venomous, predator defense posture	
Loris tardigradus	90	0	2	0	0	2	1	0	1	1	1	4		Sleeps in dense tangles, has cobra defense posture	71
L. lydekkerianus	92	0	2	0	0	2	1	0	1	1	1	4-5	Rusty spotted cat	Sleeps in dense tangles, has cobra defense posture	72; 73

0 – no evidence of use, 1 – irregular or occasional use or mixed evidence from different studies, 2 – regular or habitual use of nests, ? – evidence is based on anecdotal information or when information is lacking, * - using man-made structures as sleep sites. Social cohesion: 0 – no, 1 – yes.

(1) Charles Dominique, 1977; (2) Bearder & Honess, 1992; (3) Hohmann & Fruth, 2008; (4) Ambrose & Butynski, 2013a; (5) A. Luhrs, pers. obs.; (6) E. Pimley, pers. obs.; (7) Butynski, 1982; (8) Llorente et al., 2003; (9) Ambrose & Butynski,2013b; (10) Svensson et al., 2017; (11) Perkin, 2000; (12) Doody et al., 2001; (13) Nekaris & Bearder, 2011; (14) Butynski et al., 2006; (15) Genin et al., 2016; (16) Kingdon, 2015; (17) De Jong & Butynski, pers. obs.; (18) Honess, Perkin &Butynski, 2013; (19) McGrew, Tutin & Baldwin, 1978; (20) Nishida et al., 1979; (21) Uehara, 1997; (22) Pruetz & Bertolani, 2007; (23) Off, Isbell, & Young, 2008; (24) De Jong & Butynski, 2009; (25) O'Malley, 2010; (26) Nash, Zimmer-mann & Butynski, 2013; (27) Svensson & Bearder, 2013; (28) Butynski & De Jong, 2014; (29) Butynski & De Jong, 2017; (30) Pruetz et al., 2015; (31) Butynski & De Jong, 2004; (32) Butynski & De Jong, 2013; (33) De Jong & Butynski,2004a; (34) De Jong & Butynski, 2004b; (35) De Jong & Butynski, 2010; (36) Mzilikazi, Masters & Lovegrove, 2006; (37) Nowack, Mzilikazi & Dausmann, 2010; (38) Burnham et al., 2012; (39) Baker, 2013; (40) Nowack, Wippich, Mzilikazi,& Dausmann, 2013b; (41) Pullen & Bearder, 2013; (42) Ambrose, 2006; (43) Pimley, 2002; (44) Ambrose & Pimley, 2013; (45) Ambrose, 2013; (46) Nekaris, 2013b; (47) Ambrose, 2003; (48) Ambrose, 2013; (49) Ambrose & Oates, 2013;(50) Rovero, Marshall, Jones & Perkin, 2009; (51) Lumsden & Masters, 2001; (52) De Jong & Butynski, 2009; (53) Harcourt & Perkin, 2013; (54) Hart, Katembo & Punga, 1996; (55) Msuya, 1993; (56) Shultz, NoÞ, McGraw, & Dunbar,2004; (57) Pimley & Bearder, 2013; (58) Pimley, Bearder & Dixson, 2005a; (59) Pimley, Bearder & Dixson, 2005b; (60) Nekaris et al., 2017; (61) Das, Nekaris, & Poindexter, pers. obs.; (62) Stark, pers. obs.; (63) Kenyon et al., 2014; (64)Nekaris & Poindexter, pers. obs.; (65) Wiens & Zitzmann, 1999; (66) Moore, pers. comm.; (67) Utami & van Hooff, 1997; (68) Hardus et al., 2012; (69) Schuppli, pers. comm.; (70) Nekaris & Nijman, pers. obs.; (71) Nekaris & Jayewardene,2003; (72) Bearder, Nekaris & Buzzell, 2002; (73) Nekaris, 2003b.

from sleep sites in bamboo and dense tangles and the use of nests should be interpreted very loosely due to a lack of signal.

At ~40 Mya (range 36–44 Mya, nb. all dates used herein are taken from Pozzi et al., 2015), we suggest that the ancestral lorisiform infant was carried by clinging to the fur of its parent (Figure 1). This ancestral state is retained in all Asian taxa as well as in some African taxa (e.g., *Perodicticus*, *Arctocebus*, and *Otolemur*). We propose that carrying infants in the mouth evolved ~22 (17–26) Mya in the ancestor of the African galagos. We assume that the ancestral lorisiform used dense tangles and branches/forks as sleep sites. Almost all extant species still use dense tangles as sleep sites, but we suggest that this trait was lost twice in the east African coastal *Paragalago* species. While the majority of species still use branches/forks as sleep sites, we propose that this trait changed at ~14 (12–18) Mya for *Paragalago* and ~12 (8–15) Mya, when *Otolemur* and *Sciurocheirus* split from the other galagos (Figure 2).

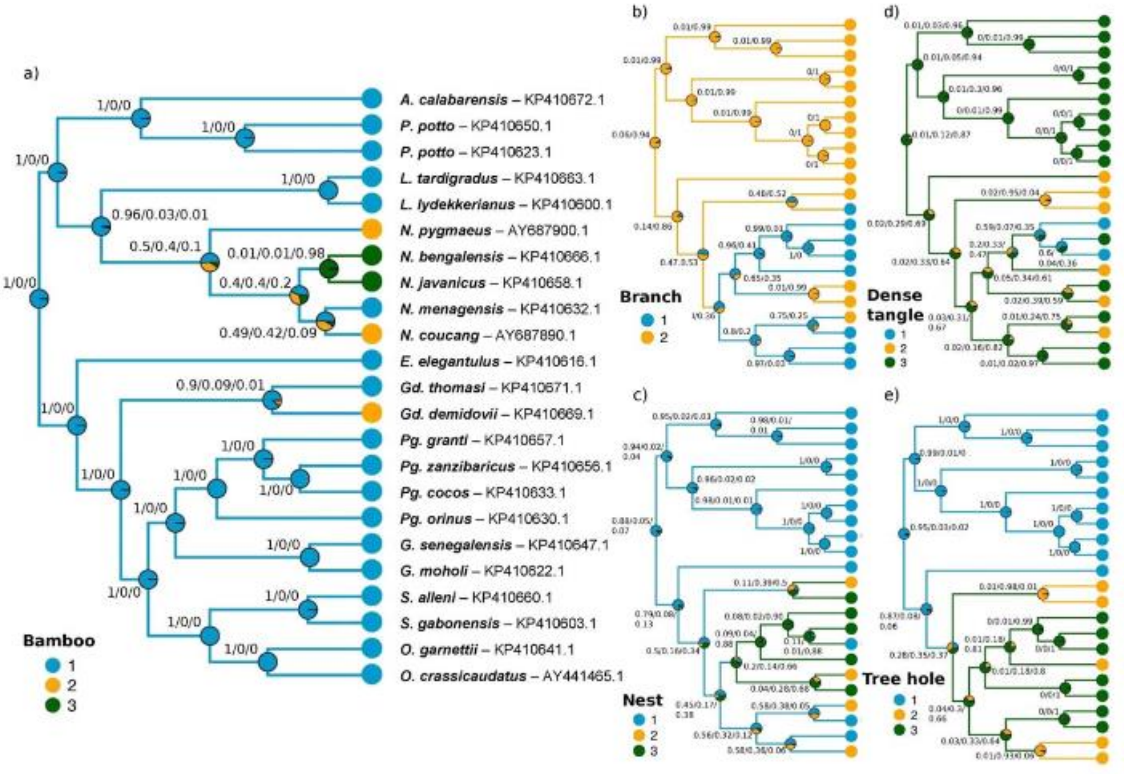

Figure 2 Ancestral state reconstructions of stochastic character mapping of lorisiform sleep site use: (a) bamboo, (b) branch, (c) dense tangle, (d) nest, (e) tree hole. Branches above nodes (closer to tips) are colored based on their ancestral state probability. Pie charts on nodes and black numbers (states 1/2/3) indicate the probability of the state in the common ancestor. The states are in the following order: 15 = absent, 25 = occasionally present, 35 = present; except for the branch sleep site where: 15 = absent, 25 = present

The use of nests is restricted to the African lorisiforms and likely emerged 22 (17–26) Mya, after *Euoticus* split from other galagos (Figure 2). Use of bamboo as a sleep site appears to have emerged early on in their evolution at ~11 (7–14) Mya, after *Nycticebus* split from *Loris*. At present, all *Nycticebus* species, apart from *N. menagensis*, are known to use bamboo as sleep sites. Independently, *Gd. demidovii* uses bamboo as a sleep site but bamboos are absent over most of its geographic range; this behavior probably emerged in the last 5 million years.

3.2 Sleep patterns

Most lorisiforms enter their sleep site between 0.5 hr before and 0.5 hr after sunrise, and leave their sleep site between 0.5 and 1.0 hr before and 0.5 and 1.0 hr after sunset. Several lorisiforms are active (moving, feeding, and calling) during twilight: e.g. *N. javanicus* and *O. garnettii* up to 1.5 hrs before sunset, and *S. alleni*, *Pg. cocos*, *Pg. zanzibaricus* and *G.senegalensis* up to 1.0 hr before sunset.

In Africa, the number of daylight hours (time between sunrise and sunset), and thus the numbers of hours available for sleep, varies between ~13 hrs (June) and ~11 hrs (December) in Senegal and Eritrea, ~10 hrs (June) and ~14 hrs (December) in southern Africa, and ~12 hrs (year-round) in East Africa (Kenya, Tanzania and Uganda). We found no evidence that species in the more northern or southern regions adjust their sleep pattern. In general, for most species, sleep is an equitable 12 hrs year-round. In Asia, *N. bengalensis* in northeastern India, Myanmar and China, have ~10 hrs of daylight available for sleep in December and ~14 hrs in June; again, we found no evidence to suggest that they adjust their sleep pattern. The southern-most populations of lorisiforms in Asia are found in Sri Lanka (*Loris tardigradus*) and Java (*N. javanicus*), both situated ~78north and south of the equator, respectively. As such, annual variation in daylight hours is small and sleep is equitable 12 hrs year-round.

Numerous lorisiforms, including *N. javanicus*, *G. gallarum*, *G. senegalensis* and *O. garnettii* are sometimes active during the day, presumably only for short periods and possibly in response to being disturbed by humans, adverse weather or because of (real or perceived) predator threats. *Galago senegalensis* occasionally sleep in the middle of the night, but the lengths of these sleep bouts remain unknown. Additionally, *G. moholi*, N. *javanicus* and *N. pygmaeus* occasionally sleep during the night. These species have been known to use daily and multiday torpor, which may suggest they are indeed in a state of torpidity, and not sleeping (Nowack, Mzilikazi, & Dausmann, 2013a; Reinhardt, Wirdateti, & Nekaris, 2016; Ruf, Streicher, Stalder, Nadler, & Walzer, 2015). Overall, however, the daytime is used for sleeping and we could classify no species as cathemeral or polycyclic.

3.3 Predation at sleep sites

Predation avoidance appears to be a main factor in sleep site choice. Benefits are associated with all the sleep site types regarding protection against predation. Known predators of lorisiforms include a wide range of species, including those that target lorisiforms at theirsleep sites (Table 1). Snakes and monitor lizards can access tree holes and branches/forks, whereas monkeys and apes, and possibly also some snakes, can access tree holes and tangles. Among reptiles, monitor lizards *Varanus* spp. and reticulated python *Malayopython reticulatus* prey on *N. pygmaeus* and *N. coucang*. The smoothness of bamboo stems may provide protection for *Nycticebus* spp. and *Gd.demidovii*.

Diurnal raptors prey on lorisiforms, although recorded captures are scarce. Raptors known to prey on lorisiforms are: crowned eagles *Stephanoaetus coronatus* on *P. potto* and *Galago* spp., Verreaux's eagle *Aquila verreauxii* on *G. moholi*, and changeable hawk-eagle *Nisaetus cirrhatus* on *N. coucang*. These captures likely took place during the day when the lorisiforms were at their sleep site.

Small mammalian carnivores, such as palm civets, linsangs and genets (Viverridae), may capture lorisiforms when they enter or leave their sleep sites. Remains from *P. ibeanus* have been found in leopard *Panthera pardus* scats and African palm civets *Nandina binotata* are known predators of *P. edwardsi*.

Blue monkeys *Cercopithecus mitis* prey on *Gd. Thomasi* and/or *G.matschiei*, with predation observed in the afternoons. Sooty mangabeys *Cercocebus atys* have been observed poking *Gd. demidovii* out of their nests with sticks. On Sumatra *Nycticebus hilleri* has been observed to be captured and killed during daytime by *P. abelii* — we obtained confirmation from two sites—whereas there are no indications thus far that further south on Sumatra that *N. coucang* is eaten by *P. tapanuliensis* (Table 2). Data from Borneo indicate that predation on *Nycticebus* spp. by *P. pygmaeus* is less frequent, as we only were able to get confirmation of one species, *N. menagensis*, being eaten at one site (Table 2). *Pan troglodytes* occasionally prey on Galagidae (Figure 3), mainly when sleeping in tree holes, sometimes using tools such as sticks. *Pan paniscus* have been observed to force *Gd. demidovii* out of tree holes by inserting fingers into the hole and then hitting the trunk (Table 2).

Table 2 Day-time predation of lorisiforms by great apes

Species	Site, country	Predation	Reference
Pan paniscus	Lui Kotale, DR Congo	***Galagoides demidovii*** forced out of tree hole	Hohmann & Fruth, 2008
P. troglodytes	Gombe Stream, Tanzania	***Galago senegalensis*** retrieved from trunk and consumed	O'Malley, 2010
P. troglodytes	Fongoli, Senegal	***G. senegalensis***, frequently hunted, chimpanzees using tools	Pruetz & bertolani, 2007; Pruetz at al., 2015
P. troglodytes	Mt. Assirik, Senegal	***G. senegalensis*** and ***Perodicticus potto***, remains found in fecal samples	McGrew at al., 1978
P. troglodytes	Mahale Mountains, Tanzania	***Otolemur crassicaudatus*** and ***Galago spp***. harassed and consumed by chimpanzees	Nishida et al., 1979; Uehara, 1997
P. troglodytes	Haute Niger, Guinea	**Galagos**. Chimpanzees observed killing, but not consuming, galagos	C. Colin, pers. comm.
P. troglodytes	Ngogo / Kanyawaya, Kibali, Uganda	***Galago* spp**. and ***Perodicticus ibeanus***. Interactions with galagos frequently observed. Female chimpanzee offspring carried dead galago, treated it like a baby	J. Negrey, pers. comm.; R. Wrangham, pers. comm.
P. troglodytes	Bossou forest, Guinea	***P. potto*** harassed by chimpanzees	K. Hockings, pers. comm.
P. troglodytes	Tai, Ivory Coast	***P. potto***, females and offspring observed to hunt and feed on pottos	L. Luncz, pers. obs.; E. Pimley, pers. obs.
Pongo abelii	Ketambe, Indonesia	***Nycticebus hilleri***, observations of orangutans eating slow lorises	Utami & van Hooff, 1997; Hardus et al., 2012, S.S. Utami Atmoko, pers. comm.; S. Rimba, pers. comm.
P. abelii	Suaq, Indonesia	***N. hilleri***, observations of orangutans harassing and eating slow lorises	C. Schuppli, pers. comm.
P. pygmaeus	Tuanan, Indonesia	***N. menagensis***, observation of orangutan eating a slow loris	E. Vogel, pers. comm.

Humans are probably one of the main predators of lorisiforms. This relationship is especially true in Asia where *Nycticebus* and *Loris* are taken to meet the demand for the pet and traditional medicine trades, and where specialized hunters seek out sleep sites during the day.

Figure 3 Young chimpanzee Pan troglodytes in Guinea holding a dead northern lesser galago Galago senegalensis, having caught it in the daytime. Photo by: Chimpanzee Conservation Center/Charlotte Houpline

4. Discussion

We show that lorisiforms use a wide range of sleep sites, with most taxa sleeping in dense tangles, followed by holes and on branches/forks. Fewer species use nests and bamboo. It appears that the ancestral lorisiform would have used dense tangles, and branches/forks as sleep sites. We suggest that the use of tree holes and nests as sleep sites emerged ~30 (24–36) Mya in Africa, and the use of bamboo as asleep site emerged ~31 (23–26) Mya in Asia and later in Africa. The ability of infants to cling onto their parents' fur appears to be the ancestral condition, and carrying infants in the mouth is a derived condition and emerged in the African taxa. Our data provide support for Kappeler's (1998) hypothesis that use of nests and tree holes is linked to having altricial infants that are not able to cling to fur, thus providing them with a relatively safe location while adults forage.

Further understanding the comparative morphology of fur clingers may help us to infer nest using behavior in the fossil record. We found a strong relationship between more generalized arboreal lorisiforms absence of nest use and presence of infants that fur cling. Tree hole use was limited to animals with the lowest IMIs that are generally vertical clingers and leapers. Functionally, animals with shorter arms, and hence lower IMI, might not be able to cling as well on tangles and branches. Such morphological adaptations are further emphasized by the presence of a *retia mirabilia* (where the arteries form vascular bundles that allows blood to flow even when the animal remains still) in *Loris*, *Nycticebus* and *Perodicticus* allowing an enhanced grip (Ankel-Simons, 2007; Congdon & Ravosa, 2016). In the fossil record IMI and the ability to engage in specialized grasping may help us to interpret the sleeping patterns and sleep site selection of extinct species such as *Carpolestes simpsoni*, that resemble the more generalized arboreal lorisiforms in this study that did not use tree holes (Bloch & Boyer, 2002).

Sleep site selection can be seen partly as an anti-predation strategy, depending on predator species and densities (Anderson, 2000; Charles-Dominique & Martin, 1972). Factors important in reducing daytime predation appear to be: connectivity of sleep trees, use of thorny bushes, nest hole entrance size and selection of dense tangles of lianas and undergrowth and smooth-surfaced substrate such as bamboo.

The entrance size of sleep holes used by lorisiforms tends to be no larger than is necessary for the individual to enter. This minimizes the number of predator species that can enter or reach inside. Selection of tree holes with suitably small entrances that only enable the strepsirhine to enter/exit is not always possible, especially when the number of trees holes in an area is limited. As a result, holes with larger entrances are sometimes used. For example, *S. cameronensis* used tree holes with entrances of 20-cm diameter larger than necessary for it to access the hole (Pimley, 2002). More studies that systematically measure tree holes used by lorisiforms are needed.

Many species reuse sleep sites in an unpredictable order. This reuse allows them to become familiar with the sleep site and facilitate escape during predation attempts (Di Bitetti, Vidal, Baldovino, & Benesovsky, 2000; Nekaris, 2003a; Qihai, Chengming, Ming, & Fuwen, 2009; Svensson & Bearder, 2013). Rotation of sleep sites makes it more difficult for predators to ambush prey (Di Bitetti et al., 2000). Other species, such as *G. gallarum*, frequently sleep on branches/forks in the center of trees or bushes among a barrier of dense thorns, and use such areas on consecutive days (Butynski & De Jong, 2013; DeJong & Butynski, 2004a, b). Sleeping in tangles of dense vegetation reduces detection from predators, provides protection from the elements and facilitates rapid escape, especially for smaller lorisiforms such as *Galagoides*, *Paragalago* and *Loris* (Kappeler, 1998). Vegetation tangles and bamboo have also been hypothesized as anti-predation strategy for *Loris* and *Nytcicebus* (Nekaris, 2014). The slow and slender lorises, angwantibos and pottos are nonsaltatory arboreal climbers, incapable of leaping (Sellers, 1996). This locomotion demands constant connectivity to maintain substrate contact, as well as an increased number of escape routes from predators (Voskamp, Rode, Coudrat, Wilson, & Nekaris, 2014).

Researchers have found animals exposed to high levels of predation to display less time spent in sleep, while those with less disturbances experience increased sleep quality (Samson & Shumaker, 2013, 2015a). This behavior is largely due to disturbances from predators during the sleeping period, as well as a need to be more alert (Lima, Rattenborg, Lesku, & Amlaner, 2005; Zepelin, 2000). More field research on sleep quality is needed in primates, to determine if different sleep site types and predation pressures influence sleep patterns.

The use of different types of sleep sites within the same species of lorisiform suggests these species may be opportunistic generalists that are able to use the range of habitat features available to them or respond to varying sleep site selection pressures. Similar variability is seen in other primate species that have access to the same types of sleep sites in different environments, but do not select them based on differences in the site characteristics (Duarte & Young, 2011; Pontes & Soares, 2005). Despite the range of sleep site types seen across the group however, sleep patterns are mostly consistent, with all species demonstrating nocturnal, not cathemeral behavior.

Given that most lorisiforms live in the tropics and only a few in the subtropics, with small amounts of variation in day length, most species have equal amounts of time available for sleep. The exceptions are *N.bengalensis*, and the southern-most populations of *G. moholi* and *O.crassicaudatus*, which have 4 hrs less available for sleep in winter than in summer (for *N. bengalensis* this is the boreal winter and for *G. moholi* and *O. crassicaudatus* it is the austral winter, when nights are significantly longer than in the summer). Several species of lorisiform are active for short periods during the day (Bearder, Nekaris, & Curtis, 2006). These patterns are possibly linked to low temperatures or other adverse conditions.

Thermoregulation may be an important factor in sleep site selection in lorisiforms, especially for species that live at high elevations and/or at high or low latitudes (Ruf et al., 2015). Tree holes provide good insulation against the cold (Dausmann, Glos, Ganzhorn, & Helmaier, 2004; Schmid, 1998), and buffer against heat. Nests may also serve thermoregulatory requirements (Lutermann, Verburgt, & Rendigs, 2010; Nowack et al., 2013a; Radespiel, Cepok, Zietemann, & Zimmermann, 1998). *Galago moholi* return to their sleep site (usually a treehole but also nests) earlier than usual during cold nights to huddle with other individuals thus serving a thermoregulatory purpose (Bearder &Martin, 1980). The requirement for thermoregulation may also explain why the smaller species of lorisiform such as *Loris*, *Galago*, *Galagoides*, *Paragalago* and *Sciurocheirus* (which lose heat more quickly than their larger relatives) tend to sleep together, thereby sharing body heat (Nowack, Wippich, Mzilikazi, & Dausmann, 2013b; cf. Eppley, Watzek, Dausmann, Ganzhorn, & Donati, 2017). Some of these smaller taxa, including *Pg. zanzibaricus* and *Gd. thomasi*, bring in fresh plant material to line their sleep site (Bearder et al., 2003).

Peckre et al. (2016) pointed out the need for more studies on infant carrying and its relevance to primate evolution, in particular regarding the evolution of an enhanced grip. Based on nearly 20 years of new field data, we help to confirm the view that fur clinging is an ancestral trait in lorisiforms, and that fur clinging species rarely or never use tree holes (cf., Kappeler, 1998). Lorises and pottos have a shared derived trait called the *retia mirabilia*, as well as a reduced second digit (Ankel-Simons, 2007). These morphological traits produce an enhanced grip that has been suggested to be an anti-predation strategy (Charles-Dominique, 1977; Nekaris, 2014; Oates, 1984). Where in-depth studies were conducted on apes, the importance of sleeping posture has proven to improve sleep quality (Samson & Shumaker, 2013, 2015a). Similarly, clinging to branches and a strong grip is also shown to be related to continuous sleep during the diurnal period as well as a decreased frequency of measurable fragmented sleep (KAIN and KDR, unpublished data). The confirmation of nest use as a derived state in strepsirhines that evolved multiple times corresponds with the deep evolutionary divergence seen among lemuriforms and lorisiforms. We provide a novel set of data that we hope will inform further studies reconstructing aspects of primate evolution.

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