International Journal of Primatology (2024) 45:1309–1319
https://doi.org/10.1007/s10764-024-00476-w

Introduction to the Special Issue on What They Do in the Shadows: New Perspectives on Africa's Nocturnal Bushbabies

Frank P. Cuozzo[1,2] · Michelle L. Sauther[3] · Luca Pozzi[4] · John K. Dalton[3]

Accepted: 15 November 2024 / Published online: 11 December 2024

Among continental Africa's endemic primates, the bushbabies or galagos (family Galagidae, or Galonigidae, Groves, 2001) have been described as the most successful radiation of strepsirrhine primates in terms of species diversity and geographic range (Fleagle, 2013; Nekaris & Bearder, 2011). Currently, more than two dozen species have been named across six genera (Penna & Pozzi, 2024). All members of this clade are nocturnal (Bearder, 1999), in contrast to the lemurs of Madagascar (which include nocturnal, diurnal, and cathemeral species; LaFleur *et al*., 2014) and the haplorrhine primates, with two nocturnal taxa (Southeast Asia's tarsiers, and South America's owl monkeys; Fleagle, 2013). Along with the lorisids and Malagasy lemurs, the strepsirrhine primates (previously the prosimian primates, minus Southeast Asia's tarsiers) have been described, and long viewed, as the "poor sister group" of the primates (Martin, 1993:192). This can be seen in the contrasting large number of publications on the anthropoid (i.e., haplorrhine [monkeys and apes plus the tarsiers]) primates, especially the great apes and baboons (Sauther *et al*., 2015). What follows is an introduction to a special issue on the galagos/bushbabies. This introduction puts the special issue into context, by providing a short history of the study of this group, a summary of their evolution and divergence from other primate clades, comments on their conservation status, and brief synopses of the papers included in this volume.

Handling Editor: Joanna M. Setchell

✉ Frank P. Cuozzo
makiteeth@hotmail.com

[1] Department of Zoology and Entomology, Mammal Research Institute, University of Pretoria, Pretoria, South Africa

[2] Lajuma Research Centre, Lajuma, South Africa

[3] Department of Anthropology, University of Colorado-Boulder, Boulder, CO, USA

[4] Department of Anthropology, University of Texas-San Antonio, San Antonio, TX, USA

A Short History of the Study of Galagos

Most behavioral and ecological research on galagids occurred during the 1970s and 1980s. Many of these studies of behavioral ecology, including feeding, locomotion, and social organization, were short-term, and often advanced graduate student projects (Bearder, 1974; Bearder & Doyle, 1974; Bearder & Martin, 1980; Harcourt, 1980, 1986; Harcourt & Nash, 1986; Masters *et al*., 1988; Nash, 1986). This initial period of study developed as part of a more systematic and quantitative primatology, also seen in the study many other primate groups, including apes, baboons, and some lemurs. However, longitudinal data on Africa's bushbabies remained limited until very recently, in contrast to several sites where work on single or multiple lemur species now includes several decades of longitudinal data (Sauther *et al*., 2015; Gould & Sauther, 2006; Goodman & Ganzhorn, 2022). There is far less research on galagos than on some haplorrhine primates (e.g., apes and baboons) and on Malagasy strepsirrhines, especially *Lemur catta* (Jolly, 1966; Jolly *et al*., 2006; Sauther & Cuozzo, 2022; Sauther *et al*., 2015) but also other lemur species (Tattersall, 1982; Gould & Sauther, 2006; Goodman & Ganzhorn, 2022).

Most of the work published on galago behavior and ecology between 1971 and 2020 focused on the genus *Otolemur* (prior to Olson, 1979 and Nash *et al*., 1989, all *Otolemur* species were included in the genus *Galago*) (Ellison *et al*., 2021). A rapid increase in published studies of galagos began in the late 1990s (Ellison *et al*., 2021). However, despite the overall increase, this more recent work on galagos is dominated by publications focused on the smaller galagids, especially taxonomy and systematics, with far fewer studies on *Otolemur.*

Galago Evolution

The divergence of the earliest galagids from their sister taxa (the African and Asian lorisids), and other nonhuman primates, dates to the latter part of the Eocene Epoch (Sieffert *et al*., 2003; Sieffert, 2007). For example, a stem galagid (*Saharagalago*) is thought to have diverged from the stem lorisids during this time (Sieffert *et al*., 2003), a date confirmed by more recent molecular data (Pozzi *et al*., 2014). Although temporally discontinuous, the galagid fossil record also includes early dwarf, lesser, and greater galagids from the Miocene and Pliocene Epochs, sometimes found in fossil deposits that include early hominoids and hominids (Fleagle, 2013; Kunimatsu *et al*., 2017; Phillips & Walker, 2002). For example, a fossil galagid from the Upper Pliocene (*Galago howelli*) from the well-known fossil hominid site of Omo, Ethiopia, is described as being similar in morphology to living *Galago alleni* and *Galago crassicaudatus* (the latter now placed in the genus *Otolemur* [Olsen, 1979; Nash, Bearder, & Olsen, 1989]).

The taxonomy of the galagids remained fairly stable from their first description(s) in the nineteenth century, with only two genera recognized well into the twentieth century by Schwarz (1931) (Bearder, 1999; Groves, 2001). Olson (1979) and Nash *et al*. (1989) resurrected the genus *Otolemur* for the greater or thick-tailed galagos in the 1970s and 1980s. Following this work, the overall taxonomy greatly expanded with the identification of numerous species, especially among the lesser and dwarf groups (Masters, 1998). A number of new dwarf galago species were named in the 1990s (Honess & Bearder, 1996; Wickings *et al*., 1998). A new dwarf galago genus was named more recently, including the dwarf forms along Africa's eastern coast, with a number of new species within this group (i.e., *Paragalago*) in the 2010s (Genin *et al*., 2016; Masters *et al*., 2017; Penna & Pozzi, 2024). This rapid taxonomic expansion parallels that of the nocturnal lemurs of Madagascar over the same period, in which the sportive and mouse lemurs (the smallest lemur taxa) have seen a large increase in the number of named and generally accepted species (Tattersall & Cuozzo, 2018). In addition to new techniques and methods of analysis, including research on cryptic species, this rapid taxonomic expansion among the smaller galagos (and lemurs) may be a product of shifting perspectives, including funding sources, where there is a financial benefit in terms of conservation attention and support for species viewed as more threatened than others, often those with limited geographic ranges. This has been evident in terms of funding availability for lemur species assigned more dire IUCN status, with fewer funding opportunities for more widespread species, and those with a long history of study (Tattersall & Cuozzo, 2018).

Conservation Status

Among the more challenging issues concerning the study of galagids is the varied conservation status assigned to different taxa, ranging from Least Concern to Endangered. For example, several lesser and greater galago species are rated as Least Concern (Masters, Génin & Bearder, 2016; de Jong, Butynski, Svensson, & Perkin, 2019; Svensson & Bearder, 2019; Bearder *et al*., 2021), whereas *Paragalago rondoensis*, a species whose geographic distribution is limited to a few isolated, higher altitude, spots in Tanzania, is listed as Endangered (Perkin, 2020). Because some species are viewed as abundant, funding sources to study these taxa are limited, as funding is often dependent on a species' conservation status, an issue also seen in the study of extant lemurs (Tattersall & Cuozzo, 2018). The paucity of behavioral and ecological data for some galagid taxa, and only taxonomic data for others, has aided to this wide range of IUCN statuses, as accurate assessment of species boundaries—and thus interpreting their conservation status—depend on a wide range of data, including behavior and ecology, morphology, and genetics (Cuozzo *et al*., 2013; Tattersall & Cuozzo, 2018). Adding more complexity, is the perception—at least in South Africa—that the two widely dispersed galago species in South Africa, *Otolemur crassicaudatus* and *Galago moholi*, are common across their ranges. This is likely due in part to their frequent sighting in popular areas, such as rest camps in the Kruger National Park for the former species, and the frequent occurrence in suburban and urban areas for the latter (Cuozzo et al., 2021, 2022).

Despite the IUCN rating of Least Concern for most galago species (see https://www.iucnredlist.org/search?query=Galago&searchType=species), including both species of *Otolemur* (O. *crassicaudatus* and *O. garnetti*; Masters & Génin, 2016; de Jong, Butynski, Perkin, & Svensson 2019), recent work has documented several human induced threats to various members of this group, including both species of greater galago. Threats includes the impact of domestic dog kills, motor vehicles, fences and power lines, railways, and potentially shifting behaviors of endemic predators owing to habitat degradation and/or destruction (Philström *et al*., 2021; Linden *et al*., 2022, Cuozzo *et al*., 2020, 2021, 2022). For *Otolemur*, recent work has empirically documented the threat of both linear infrastructure such as roadways, railways, power lines, and fences (Linden *et al*., 2022) and kills by domestic dogs in Kenya (Philström *et al*., 2021) and South Africa (Cuozzo *et al*., 2020, 2022). Although empirical documentation of these threats is available for only a few of the many galago species, the implications for the entire clade are broad and may suggest that the conservation status of many of these species is not accurate, with many species understudied and thereby more accurately classified as Data Deficient rather than Least Concern.

Introduction to the Special Issue

On March 25, 2022, in Denver, Colorado (USA), at the 91st meeting of the American Association of Biological Anthropologists (previously known as the American Association of Physical Anthropologists), we convened a symposium bringing together scholars from North America, Europe, and Africa as presenters or coauthors on presentations to present research summaries and original, new data on continental Africa's bushbabies. Manuscripts included in this issue stem from that symposium and also include papers from scholars who were not able to physically attend the symposium. A total of 31 authors and coauthors (some contributing to more than one paper) based in six countries (USA, UK, South Africa, Mexico, Finland, and Kenya) are represented in the special issue. We present recent data from numerous leading researchers to better characterize and update the state of research on this enigmatic and relatively lesser-understood group of nocturnal primates.

In addition to systematics and phylogeny, the most recent research on the galagids has expanded to include longitudinal and cross-sectional data on behavior, physiology (including endocrinology), phylogenetics and species diversity, taxonomy, phylogeography, and most recently health and conservation (Nowack, 2013a, 2013b; Scheun *et al*., 2014, 2016, 2017; Strinden, 2014; Pozzi *et al*., 2014; Kotze *et al*., 2016; Masters & Génin, 2016; Masters *et al*., 2016; Masters *et al*., 2017; Phukuntsi *et al*., 2019, 2021; Long *et al*., 2021; Cuozzo *et al*., 2021, 2022; Halajian *et al*., 2024). As with the earliest studies of the galagos, when much of the work on this group was conducted by graduate students and other younger scholars, this more recent work includes projects led by a new generation of researchers. Many of the papers included in this special issue follow the theme of applying new methods and techniques to a lesser studied primate clade. The nine papers are arranged along three broad themes: taxonomy, systematics and speciation; technological advances expanding our understanding of galagids; and ecology and biology.

Taxonomy, Systematics, and Speciation

Penna & Pozzi (2024) explore the history of systematics and phylogenetic analysis within the family Galagidae and summarize the current status of galagid taxonomy. Starting with the initial nineteenth century attempts at galagid systematics dominated by morphological analysis, the paper traces the evolution of the field up to approaches that include combining genetic data with acoustic analyses of living populations and using genetic data from museum samples to assess diversity across Galagidae. The paper provides important context for the history of galagid studies and sets a course for future analysis of galagid diversity.

Miller *et al*. (2023) examines speciation and niche differentiation in the *Paragalago zanzibaricus* cryptic species cluster of East Africa. Using climatic niche modeling, which accounts for occurrence data of the species along with geographical and bioclimatic information, the paper quantifies the extent of ecological differentiation occurring between *P. cocos, P. zanzibaricus,* and *P. granti*. The results of the analysis suggest that the three species arose through allopatric speciation complexes, providing critical context for the origins of one of the most cryptic galagid genera and providing a model for assessing speciation concepts in other galagids.

Technological Advances Expanding Our Understanding of Galagids

Primate research has advanced considerably with the application of new methods, which shows great promise for nocturnal primates, who are notoriously difficult to study. A prime example is the work by Penna *et al*. (2024) which details emerging methods of extracting DNA from museum samples. The study compares two methods of DNA extraction from museum lorisiform samples and finds that while older samples provide less concentrated DNA samples, both methods provide adequate amounts of quality DNA for phylogenetic inference. This study shows that in a field traditionally dominated by genetic data from live animals, the use of DNA samples from museum samples provides primatologists with the ability to identify the presence and patterns of parasites in identified primate populations and to better characterize galagid phylogeny.

Technological advances are also enhancing our ability to understand the interplay between environmental factors and the fecal microbiome. Long *et al*. (2023) add key information for *Otolemur crassicaudatus* and find that the galago fecal microbiome appears to exhibit plasticity to cope with seasonal changes. For example, increases in *Prevotella*, which facilitate carbohydrate metabolism, appear to be related to a shift in the diet of high-fat and sugar found in insects and gums. In addition, Firmicutes, which produce high energy short-chain fatty acids, are related to a fruit diet and are increased during periods of dietary dependence on fruits. An increase in Bacteroidetes was associated with periods of increaseed insect consumption and may relate to the need to digest insect chitin. Overall, their findings that the galago microbiota can shift with their diet demonstrate these galago's ability to use their microbiota to facilitate digestion and energy extraction from a changing food resource base.

The development of passive acoustic monitoring (PAM), which uses autonomous recorders, such as microphones to capture audio data, has been a transformative tool that is being increasingly incorporated into primate studies and is especially useful in documenting the presence of small nocturnal primates. Remote sensing via light detection and ranging (LiDAR) can characterize forest structure using lasers. Rosti *et al*. (2023) combine LiDAR and PAM to understand how environmental factors such as forest size, canopy coverage, and forest density affect *Paragalago* population density in two forests in the Taita Hills in Kenya. They found that forest size and lower levels of human disturbance were positively associated with dwarf galago abundance and that dwarf galagos prefer forests with lower tree height, possibly related to insect feeding. Using PAM, they show that the Taita Hills galagos may represent a relict population of *Paragalago cocos* and that at least one population is at risk of extinction in the near future.

Ecology and Biology

Ongoing challenges to all primates include climatic and anthropogenic factors. These potential stressors are likely to differentially affect smaller nocturnal primates compared with larger diurnal species. Scheun & Nowack (2023) explore this in an article focusing on the ecological and physiological response of one such small nocturnal primate, *Galago moholi.* They argue that this species serves as an excellent template for understanding how future environmental change may impact primate feeding ecology, reproduction, and behavioral ecology given the multiplicity of challenging factors that they are facing, including rapid urbanization and climatic changes. Scheun & Nowack highlight how fragmented habitats are a particular threat that affects galago population density, genetic diversity, and fitness and can result in changes in food resources. Physiological factors are also key. For example, although they do rarely, *G. moholi* can use torpor, which could facilitate their survival during environmental droughts. Reproductive patterns can be affected by climate change, which could also affect mating periods and hence juvenile survival. Environmental stressors could alter their physiological stress response to the detriment of reproductive function.

As in many other avenues of study, our understanding of primate ontogeny and sexual dimorphism has largely come from studies of haplorrhine primates. Leigh *et al*. (2024) add new data from a wild population of *Otolemur crassicaudatus*. Using a large sample of individually known wild-caught animals, they provide insight into the complexity of sexual size dimorphism in this strepsirrhine primate species. Using an allometric ontogenetic analysis, they found that *O. crassicaudatus* show one of the highest adult body mass sexual size dimorphism (SSD) among strepsirrhine primates, with males 1.21 times the size of females. However, body mass is decoupled from skeletal measures of SSD, meaning that body mass but not the skeletal system has been affected by sexual selection. Thus, intermale competition may have selected for body mass sexual size dimorphism by producing robust, heavy males. The authors posit that movement within an arboreal niche could result in a tradeoff between SSD and locomotion, as in *Propithecus* (Lawler *et al*., 2007). Importantly, as body mass is decoupled from skeletal dimensions, determining SSD from only skeletal lengths may not be reliable, which has important implications for the fossil record.

Comparing differently sized sympatric species facilitates our understanding of the effects of body mass on strategies to deal with environmental stressors. Sauther *et al.* (2024) investigate this by comparing two sympatric galago species, *Otolemur crassicaudatus* (1500 g) and *Galago moholi* (146 g) living in a seasonal Afromontane Forest in South Africa. They show that body mass differences have broad effects on how each species negotiates variability in temperature, food resources, moon phase, and illumination and time of night. The smaller *G. moholi* has greater energy and protein requirements, resulting in them being active across a wider range of temperatures in search of high-quality foods, such as insects. This pattern contrasts with *O. crassicaudatus*, whose larger body mass and greater fat reserves allows them to focus on gum and may buffer them and allow them to avoid both periods of high and low temperature. Predation constraints also differentially affect the two species, with *G. moholi* being lunarphilic, which helps them to visually detect insect prey and potential predators. Conversely, *O. crassicaudatus* are lunarphobic and may avoid larger predators that tend to be more active during periods of greater lunar illumination.

Understanding the socioecology of nocturnal primates continues to be challenging, given the difficulty of consistently following and collecting behavioral data; however, it is essential to test theories regarding the development of sociality in primates overall. Ellison *et al*. (2023) studied sociality in free-ranging *Galago senegalensis* in Tanzania, Senegal, and Kenya. They found differences in sociality across the populations, noting that vocalizations, rather than direct social interactions, connect individuals, which allow them to avoid costs of group-living, including predator avoidance and resource competition.

Conclusion and Dedication

The papers included in this special issue review current research in the field, present new data for a number of species, and set a course for future collaborative research on Africa's cryptic galagid primates. They also provide examples of the ways that new techniques and methods have greatly improved our knowledge of Continental Africa's cryptic, nocturnal bushbabies. These new data illustrate a new perspective and help to shift away from the outdated perspective that the study of galagos and other members of the "poor sister group" of strepsirrhine primates (Martin, 1993:192) adds little to the broader understanding of primate ecology, behavior, and evolution. The papers included in this volume—and the work reported herein—would not have been possible without the near five decades of work first carried out on Africa's bushbabies in the 1970s and 1980s. Each of us owes a debt of gratitude to the pioneers of bushbaby research, including Simon Bearder, Robin Crompton, Gerard Doyle, Caroline Harcourt, Judith Masters, Leanne Nash, and Todd Olsen (alphabetical order, see citations in Nash *et al.*, 1989). This work ranging, from baseline behavioral and ecological research, locomotion, predation, and systematics, each form the foundation(s) of current research. The editors of this volume dedicate this volume to all the above, and Judith Masters and Fabien Génin, whose untimely deaths are not only a personal but also a great intellectual loss.

Funding Open access funding provided by University of Pretoria.

References

Bearder, S. K. (1974). Aspects of the Ecology and Behavior of the Thick-tailed Bushbaby, *Galago crassicaudatus*. (Unpublished doctoral thesis). University of the Witwatersrand.

Bearder, S. K. (1999). Physical and social diversity among nocturnal primates: A new view based on long term research. *Primates, 40*(1), 267–282.

Bearder, S. K., & Doyle, G. A. (1974). Field and laboratory studies of social organization in bushbabies (*Galago senegalensis*). *Journal of Human Evolution, 3*(1), 37–50.

Bearder, S. K., & Martin, R. D. (1980). Acacia gum and its use by bushbabies, *Galago senegalensis*. (Primates: Lorisidae). *International Journal of Primatology, 1*, 103–128.

Bearder, S., Svensson, M., Butynski, T.M. & de Jong, Y.A. (2021). *Galago moholi*. *The IUCN Red List of Threatened Species* 2021: e.T8788A206563837. https://doi.org/10.2305/IUCN.UK.2021-3.RLTS.T8788A206563837.en

Cuozzo, F. P., Rasoazanabary, E., Godfrey, L. R., Sauther, M. L., Youssouf Jacky, I. A., & LaFleur, M. (2013). Biological variation in a large sample of mouse lemurs (*Microcebus griseorufus*) from Amboasary, Madagascar: Implications for interpreting variation in primate biology. *Journal of Human Evolution, 64*, 1–20.

Cuozzo, F. P., Halajian, A., Sauther, M. L., Linden, B., Linden, J., Millette, J., Tordiffe, A. S. W., & Romanello, D. (2020). Human induced threats to a nonhuman primate of "Least Concern" (Otolemur crassicaudatus, Primates: Galagidae) in northern South Africa. *American Journal of Physical Anthropology, 171*(S69), 63.

Cuozzo, F. P., Halajian, A., Sauther, M. L., Rampedi, K. M., & Millette, J. B. (2021). First report of the thick-tailed bushbaby (*Otolemur crassicaudatus*) being preyed upon by an endemic carnivore (*Caracal caracal*) in South Africa. *African Zoology, 56*(3), 231–235. https://doi.org/10.1080/15627020.2021.1949389

Cuozzo, F. P., Linden, J., Sauther, M. L., Halajian, A., & Linden, B. (2022). Domestic Dogs Present a Human-Induced Threat to Thick-tailed Bushbabies (*Otolemur crassicaudatus*) in Northern South Africa. *African Primates, 16*, 59–64.

de Jong, Y. A., Butynski, T. M., Perkin, A. & Svensson, M. (2019). *Otolemur garnettii*. *The IUCN Red List of Threatened Species* 2019: e.T15644A17963837. https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T15644A17963837.en

de Jong, Y. A., Butynski, T. M., Svensson, M. & Perkin, A. (2019). *Galago senegalensis*. *The IUCN Red List of Threatened Species* 2019: e.T8789A17963505. https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T8789A17963505.en. Accessed 12 August 2024.

Ellison, G., Jones, M., Cain, B., & Bettridge, C. M. (2021). Taxonomic and geographic bias in 50 years of research on the behaviour and ecology of galagids. *PLoS ONE, 16*(12), e0261379. https://doi.org/10.1371/journal.pone.0261379

Ellison, G., Jones, M., Cain, B., & Bettridge, C.M. (2023). Activity budget and sociality of the Northern Lesser Galago, *Galago senegalensis*. *International Journal of Primtology*. https://doi.org/10.1007/s10764-023-00406-2

Fleagle, J. G. (2013). *Primate adaptations and evolution*. Academic Press.

Génin, F., Yokwana, A., Kom, N., Couette, S., Dieuleveut, T., Nash, S. D., & Masters, J. C. (2016). A new galago species for South Africa (Primates: Strepsirhini: Galagidae). *African Zoology, 51*(3), 135–143.

Goodman, S. M., & Ganzhorn (Eds.) (2022) *The natural history of Madagascar* (2nd ed). Princeton University Press.

Gould, L., & Sauther, M. L. (2006). Lemurs: Ecology and adaptation. *Springer*. https://doi.org/10.1007/978-0-387-34586-4

Groves, C. P. (2001). *Primate taxonomy*. Smithsonian Institution Press.

Halajian, A., Cuozzo, F. P., Heyne, H., Sauther, M. L., Linden, B., Linden, J., Tordiffe, A. S. W., Rampedi, K. M., & Hornok, S. (2024). Hard ticks (*Acari:Ixodidae*) parasitizing bushbabies (Mammalia: Galagidae) in a biodiversity hotspot of northern South Africa. *Tick and Tick-borne Diseases*, *15*(2), 102313 ISSN 1877–959x. https://doi.org/10.1016/j.ttbdis.2024.102313

Harcourt, C. S. (1980). *Behavioural adaptations in South African galagos*. (unpublished MA thesis). University of Witwatersrand.

Harcourt, C. (1986). Seasonal variation in the diet of South African Galagos. *International Journal of Primatology, 7*(5), 491–506. https://doi.org/10.1007/BF02693660

Harcourt, C. S., & Nash, L. T. (1986). Social organization of galagos in Kenyan coastal forests: I. *Galago Zanzibaricus. American Journal of Primatology, 10*(4), 339–355. https://doi.org/10.1002/ajp.1350100406

Honess, P. E., & Bearder, S. K. (1996). Descriptions of the dwarf galago species of Tanzania. *African Primates, 2*, 75–79.

Jolly, A. (1966). Lemur behavior: A Madagascar field study. University of Chicago Press.

Jolly, A., Sussman, R. W., Koyama, N., & Rasmimanana, H. (2006). *Ring-tailed biology*. Springer

Kotze, A., Dalton, D. L., Strinden, M., Sauther, M. L., Cuozzo, F. P., & Stone, A. C. (2016). An evaluation of the oral microbiome and potential zoonoses of the thick-tailed or greater galago (*Otolemur crassicaudatus*). *African Primates, 11*, 19–26.

Kunimatsu, Y., Nakatsukasa, M., Sakai, T., Saneyoshi, M., Sawada, Y., & Nakaya, H. (2017). A newly discovered galagid fossil from Nakali, an early Late Miocene locality of East Africa. *Journal of Human Evolution, 105*, 123–126. https://doi.org/10.1016/j.jhevol.2017.02.003

LaFleur, M., Sauther, M. L., Cuozzo, F. P., Yamashitay, N., Jacky Youssouf, I. A., & Bender, R. (2014). Cathemerality in wild ring-tailed lemurs (*Lemur catta*) at Tsimanampetsotsa National Park in southwestern Madagascar. *Primates, 55*, 207–217.

Lawler, R. R. (2007). Fitness and extra-group reproduction in male Verreaux's sifaka: An analysis of reproductive success from 1989 to 1999. *American Journal of Physical Anthropology, 132*, 267–277. https://doi.org/10.1002/ajpa.20507

Leigh, S.R., Sauther, M.L., Cuozzo, F.P., Tordiffe, A.S.W., & Van Wyk, I. (2024). Size, scaling, and sexual size dimorphism in wild South African thick-tailed greater galagos (*Otolemur crassicaudatus*). *International Journal of Primtology*. https://doi.org/10.1007/s10764-024-00466-y

Linden, B., Cuozzo, F. P., Sauther, M. L., & Jonker, W. C. (2022). Impact of linear infrastructure on South Africa's primate fauna: the need for mitigation. *Folia Primatologica*, *93*:235–253.

Long, C., Tordife, A., Sauther, M., Cuozzo, F., Millette, J., Gandwindt, A., & Scheun, J. (2021). Seasonal drivers of faecal glucorticoid metabolite concentrations in an African strepsirrhine primate, the

thick-tailed galago (*Otolemur crassicaudatus*). *Conservation Physiology*, 9(1), coab081. https://doi.org/10.1093/conphys/coab081
Long, C., Scheun, J., Sauther, M.L., Cuozzo, F.P., Millette, J., & Tordiffe, A.S.W. (2023). Seasonal effects on the fecal microbial composition of wild greater thick-tailed galagos (*Otolemur crassicaudatus*). *International Journal of Primatology*. https://doi.org/10.1007/s10764-023-00407-1
Martin, R. D. (1993). Studies of the "Poor Sister Group." *Evolutionary Anthropology, 2*, 192–195
Masters, J. C. (1998). Speciation in the lesser galagos. *Folia Primatologica, 69*(Suppl. 1), 357–370. https://doi.org/10.1159/000052724
Masters, J. C., Lumsden, W. H. R., & Young, D. A. (1988). Reproductive and dietary patterns in wild greater galago populations. *International Journal of Primatology, 9*, 573–592.
Masters, J., Génin, F., & Bearder, S. (2016). A conservation assessment of *Galago moholi*. In M. F. Child, L. L. Roxburgh, S. E. Do Linh, D. Raimondo, & H. T. Davies-Mostert (Eds.), *The Red List of mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust.
Masters, J. & Génin, F. (2016). A conservation assessment of *Otolemur crassicaudatus*. In M. F. Child, L. Roxburgh, E. Do Linh San, D. Raimondo, & H. T. Davies-Mostert (Eds.), *The Red List of mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
Masters, J. C., Génin, F., Couette, S., Groves, C. P., Nash, S. D., Delpero, M., & Pozzi., L. (2017). A new genus for the eastern dwarf galagos (Primates: Galagidae). *Zoological Journal of the Linnean Society, 181*, 229–241.
Miller, E., Luhrs, A., Mancini, A., Blair, M. E., & Pozzi, L. (2023). Assessing ecological divergence and speciation scenarios of the *Paragalago zanzibaricus* species complex through climatic niche modeling. *International Journal of Primatology*. https://doi.org/10.1007/s10764-023-00374-7
Nash, L. T. (1986). Infuence of moonlight level on traveling and calling patterns in two sympatric species of Galago in Kenya. In D. Taub & F. King (Eds.), *Current perspectives in primate social dynamics* (pp. 357–367). Van Nostrand Reinhold Co.
Nash, L., Bearder, S., & Olson, T. (1989). Synopsis of galago species characteristics. *International Journal of Primatology.*, *10*, 57–80.
Nekaris, K. A. I., & Bearder, S. K. (2011). The strepsirrhine primates of Asia and Mainland Africa: diversity shrouded in darkness. In C. Campbell, A. Fuentes, K. MacKinnon, S. K. Bearder, & R. Stumpf (Eds.), *Primates in perspective* (2nd ed., pp. 34–54). Oxford University Press.
Nowack, J., Wippich, M., Mzilikazi, N., & Dausmann, K. H. (2013a). Surviving the cold, dry period in Africa: Behavioral adjustments as an alternative to heterothermy in the African Lesser Bushbaby (*Galago moholi*). *International Journal of Primatology, 34*, 49–64. https://doi.org/10.1007/s10764-012-9646-8
Nowack, J., Dausmann, K. H., & Mzilikazi, N. (2013b). Nonshivering thermogenesis in the African lesser bushbaby, *Galago moholi*. *The Journal of Experimental Biology, 216*(20), 3811–3817. https://doi.org/10.1242/jeb.089433
Olson, T. R. (1979). *Studies on aspects of the morphology of the genus Otolemur Coquerel, 1859*. (Unpublished PhD Thesis) University of London.
Penna, A., Pozzi, L. (2024). Hidden in the dark: A review of galagid systematics and phylogenetics. *International Journal of Primatology*. https://doi.org/10.1007/s10764-024-00430-w
Penna, A., Blair, M.E., Lui, HL., Peters, E., Kistler, L., & Pozzi, L. (2024). Overcoming challenges to extracting and sequencing historical DNA to support primate evolutionary research and conservation, with an application to galagos. *International Journal of Primatology*. https://doi.org/10.1007/s10764-024-00429-3
Perkin, A. (2020). *Paragalago rondoensis*. *The IUCN Red List of threatened species* 2020:e. T40652A17962115. https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T40652A17962115.en
Phillips, E. M., & Walker, A. (2002). The Fossil Lorisoids. In W. Hartwig (Ed.), *The primate fossil record* (pp. 83–95). Cambridge University Press.
Philström, H., Rosti, H., Lombo, B. M., & Pellikka, P. (2021). Domestic dog predation on white-tailed small-eared galago (*Otolemur garnettii lasiotis*) in the Taita Hills, Kenya. *African Primates, 15*, 31–38.
Phukuntsi, M. A., Du Plessis, M., Dalton, D. L., Jansen, R., Cuozzo, F. P., Sauther, M. L., & Kotze, A. (2019). Population genetic structure of the thick-tailed bushbaby (*Otolemur crassicaudatus*) from the Soutpansberg Mountain range. *Northern South Africa, Based on Four Mitochondrial DNA Regions, Mitochondrial DNA Part A*,. https://doi.org/10.1080/24701394.2019.1694015

Phukuntsi, M. A., Du Plessis, M., Dalton, D. L., Jansen, R., Sauther, M. L., Cuozzo, F. P., & Kotze, A. (2021). Population and genetic structure of a philopatric species, *Galago moholi* (Primates, Galagidae), from northern South Africa, inferred from mitochondrial DNA. *Primates*. https://doi.org/10.1007/s10329-021-00912-y

Pozzi, L., Disotell, T. R., & Masters, J. C. (2014). A multilocus phylogeny reveals deep lineages within African galagids (Primates: Galagidae). *BMC Evolutionary Biology, 14*, 72.

Rosti, H., Heiskanen, J., Bearder, S., Lombo, B., Pihlström, H., Pellikka, P., & Rikkinen, J. (2023). Distribution, population density, and behavior of dwarf galagos (*Paragalago sp.*) in Taita Hills, Kenya. *International Journal of Primatology*. https://doi.org/10.1007/s10764-023-00390-7

Sauther, M. L., & Cuozzo, F. P. (2022). Ring-tailed Lemur, (*Lemur catta*), Maky. In S. M. Goodman, J. Ganzhorn (Eds.). *The Natural History of Madagascar* (2nd ed., pp. 1952–1956). S.M. Goodman, J. Ganzhorn, (Eds.). Princeton University Press, https://press.princeton.edu/books/hardcover/9780691222622/the-new-natural-history-of-madagascar

Sauther, M. L., Gould, L., Cuozzo, F. P., & O'Mara, M. T. (2015). Ring-tailed lemurs—a species reimagined: Introduction to the symposium issue. *Folia Primatologica, 86*, 5–13.

Sauther, M.L., Millette, J.B., Cuozzo, F.P., Long, C., Msimango, V.H., & Confuron, L. (2024). Environmental effects on nocturnal encounters of two sympatric bushbabies, *Galago moholi* and *Otolemur crassicaudatus*, in a high-altitude South African Northern Mistbelt Montane habitat. *International Journal of Primtology*. https://doi.org/10.1007/s10764-024-00427-5

Scheun, J., Bennett, N. C., Ganswindt, A., & Nowack, J. (2014). Spicing up the menu: Evidence of fruit feeding in *Galago moholi*. *Primates, 55*(3), 359–363. https://doi.org/10.1007/s10329-014-0420-8

Scheun, J., Nowack, J., Bennett, N., & Ganswindt, A. (2016). Female reproductive activity and its endocrine correlates in the African lesser bushbaby, *Galago moholi*. *Journal of Comparative Physiology B, 186*(2), 255–264. https://doi.org/10.1007/s00360-015-0947-z

Scheun, J., Bennett, N. C., Nowack, J., & Ganswindt, A. (2017). Reproductive behaviour, testis size and faecal androgen metabolite concentrations in the African lesser bushbaby. *Journal of Zoology, 301*(4), 263–270. https://doi.org/10.1111/jzo.12420

Scheun, J., Nowack, J. (2023). Looking ahead: Predicting the possible ecological and physiological response of *Galago moholi* to environmental change. *International Journal of Primtology*. https://doi.org/10.1007/s10764-023-00373-8

Schwarz, E. (1931). On the African long-tailed lemurs or galagos. *Annals and Magazine of Natural History* (series 10), *7*, 41–66.

Siefert, E. R. (2007). Early evolution and biogeography of lorisiform strepsirrhines. *American Journal of Primatology, 69*(1), 27–35. https://doi.org/10.1002/ajp.20324

Sieffert, E. R., Simons, E. L., & Attia, Y. (2003). Fossil evidence for an ancient divergence of lorisies and galagos. *Nature*, 422–424.

Strinden, M. K. (2014). *An evaluation of the oral microbiome and potential zoonoses of two ubiquitous South African Strepsirrhines, Otolemur crassicaudatus* and *Galago moholi* (Unpublished Master's Thesis). University of Colorado.

Svensson, M. & Bearder, S. (2019). *Galagoides thomasi*. *The IUCN Red List of threatened species* 2019:e.T40653A17962691. https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T40653A17962691.en

Tattersall, I. (1982). *The primates of Madagascar*. Columbia University Press.

Tattersall, I., & Cuozzo, F. P. (2018). Systematics of the extant Malagasy lemurs (Order Primates). In S. M. Goodman & M. J. Raherilalao (Eds.), *In Revue des aires protégées de Madagascar/Review of the protected areas of Madagascar* (pp. 403–424). Association Vahatra & The University of Chicago Press

Wickings, E. J., Ambrose, L., & Bearder, S. K. (1998). Sympatric populations of *Galagoides demidoff* and *Galagoides thomasi* in the Haut-Ogooué Region of Gabon. *Folia Primatologica, 69*(Suppl. 1), 389–393.