

22 Directions for Future Research

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This comprehensive overview of the behavioural and ecological diversity of the colobines shows that we have greatly expanded our understanding of the taxonomy, phylogeny, morphology, natural history, behaviour and conservation status of this subfamily since Glyn Davies and John Oates (1994) published the first book on them. Nonetheless, there remain many gaps in our knowledge. In Chapter 2, Roos highlights that our current understanding of the taxonomy of colobines should be considered preliminary because classifications are still largely based on phenotypic differences between museum specimens. Changes will likely need to be implemented as data become available on ecology, behaviour, morphology and especially genetics of many species and subspecies. Roos also notes that relative to the cercopithecines, colobines are neglected in study effort and thus new findings have the potential to expand our understanding of their taxonomic diversity, especially in genera such as *Ptilocolobus*, *Colobus*, *Presbytis*, *Trachypithecus* and *Semnopithecus* that are found over large geographic areas and are species-rich. In particular, additional molecular, morphological and behavioural data are needed to stabilize the taxonomy of *Ptilocolobus* and *Trachypithecus*, which would aid in current conservation and research efforts (Chapters 15 and 21).

It should not come as surprise to anyone that more fossil specimens of colobines are needed. In Chapter 3, Frost, Gilbert and Nakatsukasa note that the fossil record of colobines from the middle Miocene of Africa has greatly expanded from what it was in the early 1990s. This means that, although we have a better understanding of colobine evolution, estimates of the split between the Cercopithecinae and Colobinae typically suggest an early Miocene divergence, leaving the first 5–7 million years of colobine evolution undocumented. The phylogenetic relationships among fossil taxa are also lacking due to few craniodental features that allow one to distinguish different clades. Roos and Zinner further highlight in Chapter 4 that the phylogenetic relationships among extant taxa are also unclear in many respects.

In Chapter 5, Wright and Willis further discuss how a lack of longitudinal studies, life history information, and dental casts in the Asian and African colobines are problematic for understanding how diet links to specific dental patterns. What has become clear over the last 25 years are that colobines contain species with varied diets, including frugivory and granivory, which should lead to variation in dental morphology. For many species, however, dental morphometrics have not been studied at all or not examined in depth. In addition, Wright and Willis layout a list

of genera where data on dental eruption, ecology, ingestive feeding, mandibular morphology, gut morphology and retention times are lacking.

In Chapter 6, Matsuda and Clauss highlight that the difficulty in keeping many species of colobines in captivity is due to our lack of understanding of their digestive physiology. The function of the praesaccus is still unknown for those species that have a quadripartite stomach arrangement. Indeed, for *Simias*, no information on the number of chambers in the stomach is even available. It is still unknown why colobines have a low degree of fluid throughput through the forestomach relative to other folivores. For most taxa, the foregut microbiome has not been characterized and related metagenomic and function analyses in relation to the environment have not been done. Amato, Clayton, and Hale (Chapter 7) reiterate this point and discuss how knowledge of specific microbial taxa and their functions in both the fore- and hindguts of colobines is in its infancy, though more is known regarding the hindgut microbiome. Captive colobines that show gastrointestinal distress often have microbiome differences compared to their healthy counterparts but it is not known if this is a cause or a symptom of the distress. Amato and colleagues suggest that routine sampling of captive colobine gut microbiomes would be very helpful in elucidating these issues and preventing the death of captive colobines. Greater understanding of the gut microbiota, diets and morphology across the subfamily may also explain why different colobine taxa show variability in gastrointestinal problems in captivity.

Rothman, DePasquale, Evans and Raboin discuss colobine nutritional ecology in Chapter 8. The authors postulate that, given their digestive anatomy, colobines seem to be able to extract nutrients from many different foods (i.e. they have a wide acceptable niche), yet they often rely on diets containing relatively few species. This suggests that the application of nutritional frameworks to colobine feeding strategies could be very informative. Many more studies are needed on the daily nutrient intake of both Asian and African colobines from a wide variety of sites. It is also still unclear how colobines select dietary items and the criteria proposed, namely the protein-to-fibre model and selection based on energy content, were both difficult to test given the previous analytical techniques. Rothman and colleagues suggest that new methods will help clarify selection criteria, and that colobines at different locations may opportunistically maximize the nutrients that are environmentally constrained whenever they become available. Due to the extreme diversity of plant secondary metabolites (i.e. tannins and phenolics), standardized analytical methods are also desperately needed to determine the actual presence of these in colobine foods and how different species cope with these. The role of micronutrients (i.e. vitamins and minerals) and the degree of their consumption is also unknown for many colobine species. Sodium-seeking has been noted in some studies and geophagy may be a common way for colobines to find micronutrients. Rothman and colleagues stress that monitoring food (and nutrient) availability over time along with nutritional chemistry would provide an ideal way to determine how colobines select plant parts and deal with changing conditions.

The taxon-specific chapters of the book demonstrate the great amount of information that we still do not know about the colobine monkeys. In the red colobus natural history chapter (Chapter 9), Korstjens, Hillyer and Koné highlight the unresolved taxonomy and the lack of basic natural history information for species and populations outside of a few intensively studied field sites. The difficulty of recognizing individuals in large red colobus groups makes collection of data on social relationships, sexual behaviour, mating strategies, receptive periods, birth rates and reproductive success challenging. Although some work has looked at the pathogens present in red colobus populations, few have linked these to their behavioural ecology. The lack of data for so many red colobus taxa is an urgent issue given how vulnerable populations can be to extirpation with increasing human habitat destruction and persecution. The natural history of the black-and-white colobus is a fraction more complete than for the red colobus but as Fashing notes in Chapter 10, there are still relatively large gaps. For instance, *C. guereza*, arguably the best studied of the black-and-white colobus is still unstudied in the western half of its distribution and even in East Africa there are isolated, genetically distinct subspecies and populations where no data are available. The important and fascinating avenues for further research that Fashing suggests are (1) a better understanding of why *C. angolensis* groups are so tolerant of one another relative to other black-and-white colobus; (2) confirmation of sympatry among some black-and-white colobus populations and studies of niche separation; (3) protection and study of remaining critically endangered *C. vellerosus* populations in continuous forest; (4) an assessment of how *C. polykomos* and *C. satanas* deal with forest fragmentation and (5) comparisons of ecology between the northern and southern populations of *C. satanas* on Bioko Island, where rainfall varies 5-fold. In the chapter on olive colobus natural history (Chapter 11), Teichroeb and Korstjens suggest several studies that would fill information gaps for this unique, monotypic species. These include a better understanding of mating strategies to determine the function of large sexual dimorphism in canine size, the presence of some features related to sperm competition, and female-mimicry in young males prior to sexual maturation. Studies that include individual recognition would be very beneficial for expanding our understanding of the enigmatic olive colobus.

Our understanding of the ecology and behaviour of the odd-nosed colobines has increased dramatically since the first book on colobines ~25 years ago; however, Grueter, Erb, Ulibarri and Matsuda emphasize several important areas where data are lacking. With the exception of golden snub-nosed monkeys, our understanding of many aspects of the social system (group stability/fluidity, dispersal patterns, group coordination, between-group interactions, social preferences and competitive regimes) of odd-nosed colobines is still rudimentary. Moreover, because of the logistical challenges of data collection in the field, the natural history of some species (in particular the critically endangered black snub-nosed monkey), is still largely unknown. In Chapter 13, Sayers points out that although grey langurs are arguably the best studied colobine monkeys, this is not true throughout their wide range and there is a dearth of long-term field research on other *Semnopithecus* taxa.

Specifically, Sayers proposes that studies on the impact of predation on grouping and behaviour, the proximate mechanisms of behaviour (e.g. genetics, physiology), ontogeny, sensory ecology and cognition are needed in this genus. In Chapter 14, Nijman underscores the need for research on several species of *Presbytis* and *Trachypithecus* for which very little natural history information is known. He also stresses that niche separation studies in areas where two or more colobines are sympatric are important, given how ecological similarity could lead to competition. Behie, Apthorp, Hendershott and Ruskin (Chapter 15) further note that *Trachypithecus* species in the Indo-Burmese region are almost all under intense pressure from high human populations that are converting habitat to agriculture and hunting. More general ecology studies have been done on the *Trachypithecus* inhabiting limestone karst forests than those in closed canopy forests. However, confusion regarding geographic distributions and taxonomy have hindered both conservation and research efforts. For several species basic data on activity budgets, ranging patterns, social organization and dispersal are still lacking and long-term studies on any species in this genus are rare.

Overviews of the socioecology of the Asian and African colobines by Sterck and Roth (Chapter 16) and Teichroeb (Chapter 17) respectively, show that early assumptions about the lack of food competition in this subfamily are not upheld. Colobine females face both scramble and contest competition for resources to variable degrees, which does lead to dominance hierarchies, albeit often subtle ones that are difficult to detect. However, the number of species for which behavioural data on individually recognized females are available is still small, making it difficult to determine the types and severity of competition experienced, or the types of hierarchies that females show and whether nepotism is occurring. In addition, often absent is an understanding of how food competition and greater foraging effort actually affects female reproductive success in the long-term. The impact of male reproductive strategies (e.g. infanticide, food defence) on females and social organization is also great in the colobines, which impacts how they fit (or do not fit) into current socioecological models. The influence that males can have on social structure and organization also makes colobines extremely interesting for future studies that could expand socioecological models.

In Chapter 18, Grueter discusses multilevel societies in the colobines and highlights that a combination of relaxed ecological constraints and social selective pressures may have played a role in the evolutionary coalescence of nuclear units into higher-tier entities. However, the multilevel systems of several taxa (three species of snub-nosed monkeys and the doucs) are insufficiently known, and many topics such as group coordination, communication, decision making, social cognition and disease transmission have received very little, if any, attention.

It is becoming critical to understand the factors determining colobine abundance given current population declines. In Chapter 19, Chapman, Corriveau, Valenta, Espinosa-Gómez and Schoof indicate that few advances in our understanding of the determinants of colobine population dynamics have been made since the Davies and Oates (1994) volume. They impart this to limited data on the effects of food

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quality, availability and competition, as well as predation and disease on colobine population dynamics. The authors also emphasize how these data deficiencies hamper our ability to predict and mitigate population declines. The conservation chapters in this book reiterate some of these points. Sha, Matsuda, Zhou, Ang and Nadler state in Chapter 20 that many species of Asian colobines are highly threatened. Their specialized ecological requirements render them vulnerable to environmental changes that are occurring at an increasing rate throughout their distribution range. Biological resource use, expansion of agriculture, aquaculture and land conversions associated with other anthropogenic activities are particularly threatening colobine habitats. The conservation of Asian colobines must focus on more effective conservation planning, including more comprehensive protected areas management, reforestation and restoration, enforcement and enactment of protection laws, sound reintroduction, captive management, education and awareness programmes aimed at long-term sustainability of wild habitats and species. In Chapter 21, Butynski and De Jong stress the number of species and subspecies of African colobines where geographic ranges are not confirmed, stating that this information, along with current population numbers, is urgent for taxa with limited distributions to fully understand their conservation status. They provide a list very useful targeted project ideas for particular areas where colobine occurrence data are lacking. Butynski and De Jong also emphasize that since most colobus monkey taxa are threatened with extinction, there is a great need for more data on their reactions to emerging threats like climate change, shifts in infectious disease prevalence, forest fragmentation and the increasing encroachment of humans. This is especially challenging given the lack of research on many African colobines including some of the most threatened. Basic natural history and abundance data are missing for colobines in large swaths of central Africa due to the many challenges of working in these often-unstable areas. This lack of knowledge greatly hampers the creation of effective conservation actions and management strategies.

We have learned a great deal about colobines in the 25 years since the first *Colobine Monkeys* book was published, but as this review shows there are still many gaps in our knowledge. Besides all those topics listed above, it is notable that when we first prepared the proposal for this book, we included a chapter on cognition in colobines. However, this chapter was not even possible to write due to the almost complete absence of data in this area. We also do not provide a chapter on colobine community ecology and their role in processes such as seed dispersal, predation and pollination because of the dearth of information on these topics. Our work on this book demonstrated that, as for most topics, the more we learn, the more obvious it is how much we do not yet know. It is thus our hope that this book informs and inspires future generations of scientists to work on this extraordinary group of animals.