

Rafael Reyna-Hurtado
Colin A. Chapman
Mario Melletti *Editors*

Movement Ecology of Afrotropical Forest Mammals



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Rafael Reyna-Hurtado dedicates this book to Edith, Aranza and Emiliano for having enjoyed with him the beauty of Africa forests.

Colin Chapman dedicates this book to all the friends who shared adventures with conservation efforts over the years, particularly Claire Hemingway and to the dedicated men and women of the Uganda Wildlife Authority.

Mario Melletti dedicates this book to his friends Gianfranco Tortellini and Giuseppe Corte to the memory of the beautiful times spent together.

Foreword

The extensive threats to the future of sub-Saharan Africa’s biodiversity cannot be overemphasized enough because the continent still has a lot of work in prioritizing these issues in urgent light. It is great to see how this book highlights the enormous challenges being faced by biodiversity against various factors across Africa and goes the extra mile in detailing the solutions that if considered can certainly alter the trajectory of the continent and the world’s future.

This book compiles exemplary studies of the movement of some African forest mammals. Primatologists have produced a wealth of information across Africa that includes information on their ecology and movement. It was great to see the acknowledgment of there being room and need for supplementary information collection on critical species on the continent, hence providing the groundwork for even more research to enhance the study further.

Researchers are now aware of how much altering extractive development patterns, foreign investment techniques, and rising human populations affect conservation outcomes. These elements are now incorporated into integrated management plans (like landscape approaches) to protect biodiversity and guarantee human welfare. Nonetheless, the complexity of integrated and adaptive conservation and management strategies, as well as the need to reconcile biodiversity conservation and ecosystem services with economic development and human health, is daunting, and likely out of reach for economically impoverished countries.

All life requires movement. It influences evolutionary pathways, ecological processes, individual fitness, and how populations respond to anthropogenic perturbation.^{1,2} As a result, movement ecology has become essential to both ecology and conservation biology. Emerging technological advances such as telemetry systems, drones, and artificial intelligence have significantly positively altered the rate

¹Nathan, R. (2008). An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences*, 105:19050–19051.

²Nathan, R., Monk, C. T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., . . . Bijleveld, A. I. (2022). Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science* 375:eabg 1780.

and quality of movement data further defining a bright future for the role of movement ecology in conservation. Globally, 60 million ha of tropical primary forest were lost from 2002 to 2019³ and 21% of this loss occurred in Africa.⁴ The forests of the Congo Basin cover 200 million ha, but it lost 16 million ha between 2000 and 2014, mostly to small-scale agriculture.⁵ As road infrastructure improves in the Democratic Republic of Congo and the Republic of Congo, forest loss in Africa is expected to increase dramatically.

On the same note, the continent's population is currently 1.4 billion and it is projected to quadruple by 2100 (UN 2015). This growing population will need energy and wood supplies 80% or more of domestic energy needs across Africa.⁶ In the Democratic Republic of Congo (DRC), fuelwood contributes 95% of energy needs, which amounts to an estimated 70 million m³ of wood each year.⁷

That said, Africa's development is non-negotiable; hence why we emphasize that conservation is a foundational strategy for meeting the challenges of climate change, charting a pathway for green growth, and stabilizing society as Africa's growing population faces massively increasing demands for food, fresh water, and energy.

Mainstreaming biodiversity conservation considerations into the productive sectors of the economy is necessary to ensure these ecosystems provide everything they can to contribute to Africa's growth and the empowerment of its people. This is what the book aims to delineate.

The effect of climate change on Africa's forests remains to be determined. However, climate change projections for Africa's rainforest regions indicate a 3–4 °C increase in temperature by 2100,^{8,9} approximately double the estimated mean surface temperature increase for the earth in general.¹⁰

³Weisse, M., & Gladman, E. (2020). *We lost a football pitch of primary rainforest every 6 seconds in 2019*. Washington, D.C: World Resource Institute.

⁴Estrada, A., Garber, P., & Chaudhary, A. (2020). Current and future trends in socio-economic, demographic and governance factors affecting global primate conservation. *PeerJ*, 8, e9816. doi:10.7717/peerj.9816.

⁵Reiche, J., Mullissa, A., Slagter, B., Gou, Y., Tsendbazar, N.-E., Odongo-Braun, C., . . . Pickens, A. (2021). Forest disturbance alerts for the Congo Basin using Sentinel-1. *Environmental Research Letters* 16:024005.

⁶Chapman, C., Abernathy, K., Chapman, L., Downs, C., Effiom, E. O., Gogarten, J., . . . Sarkar, D. (2022). The future of sub-Saharan Africa's biodiversity in the face of climate and societal change. *Frontiers in Ecology and Evolution* 744.

⁷Mayaux, P., Pekel, J.-F., Desclée, B., Donnay, F., Lupi, A., Achard, F., . . . Nasi, R. (2013). State and evolution of the African rainforests between 1990 and 2010. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368, 20120300.

⁸Zelazowski, P., Malhi, Y., Huntingford, C., Sitch, S., & Fisher, J. B. (2011). Changes in the potential distribution of tropical forest on a warmer planet. *Philosophical Transactions of the Royal Society of London* 369, 137–160.

⁹Malhi, et al. 2013; Malhi, Y., Adu-Bredu, S., Asare, R. A., Lewis, S. L., & Mayaux, P. (2013). The past, present, and future of Africa's rainforests. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 368:20120312.

¹⁰IPCC. (2021). *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*

Understanding what shapes animal movements can provide crucial insights into the management of endangered species and populations. If animals repeatedly return to locations with specific resources, it suggests that these resources are critical to manage if conservationists want to help a population maintain or recover.

It is refreshing to see the authors posit that if forest elephant movements in their present form are to be maintained, the planet's rich nations must match and surpass the impressive legislation for protected areas made by forest elephant range states in their commitment to demand and create the economic conditions needed for the sustainable management of tropical forest resources, including elephants.

The study demonstrated why understanding the movement of forest-living elephants is critical for reducing conflicts between elephants and farmers and understanding the variation between elephant herd movement and forest dynamics.

The book further exhibits that sustainable management to maintain the species' resilience to environmental changes and diseases, such as the establishment of protected corridors allowing gene flow between isolated populations, is critical to ensuring the species' long-term survival.

Animal movement data can reveal important food and mineral resources.^{11,12} For a variety of reasons, using this information in conservation efforts may be especially important in Africa. First, the United Nations has designated this as the Decade of Restoration, so funding for restoration efforts has increased significantly.

Second, because 20% of Africa's land surface (6.6 million km²) is degraded, an area twice the size of India, Africa will be a prime target for these restoration efforts.¹³ Finally, large sections of many of Africa's national parks have been logged or converted to agriculture, often during periods of political unrest. These are prime areas for reforestation efforts because the areas are still legally national parks and the people who converted the forest to agriculture have been resettled in several cases.

The book clearly demonstrates why better conservation strategies are clearly needed, particularly in Africa, which will face significant challenges in the coming decades. Movement ecology provides information that can be extremely beneficial to conservation. Exciting new avenues for gathering data on animal movement are being opened by new technologies. As a result, it emphasizes the critical need for

[Masson-Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen]. Cambridge University Press. In Press.

¹¹ Reyna-Hurtado, R., Chapman, C., Melletti, M., Mukasa, M., & d'Huart, J. (2023). *Movements patterns and population dynamics of giant forest hog groups in Kibale National Park, Uganda*. . New York: Springer.

¹² Thureau, E. B. (2023). Primate movements across the nutritional landscapes of Africa. R. Reyna-Hurtado, M. Melletti, and C.A. Chapman, editors. *Movement ecology of afro-tropical forest mammals*. New York: Springer.

¹³ Archer, et al. 2018; Archer, E., Dziba, L., Mulongoy, K., Maoela, M., Walters, M., Biggs, R., . . . Dunham, A. (2018). *Summary for policymakers of the regional assessment report on biodiversity and ecosystem services for Africa*. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services . Bonn, Germany.

increased research efforts that can lead to conservation to ensure that African forest mammals have a bright future.

I am greatly honored to have had the opportunity to review this masterwork that will surely influence the strides being made in the biodiversity and conservation sphere. Congratulations to editors Rafael Reyna-Hurtado, Colin A. Chapman, and Mario Melletti for the great work and I look forward to referencing this book in my discussions with leaders going forward.

Thank you.

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Chapter 1

What Do We Know About Mammal Movements in African Tropical Forests?



Rafael Reyna-Hurtado , Colin A. Chapman , and Mario Melletti 

Abstract Tropical forests have long fascinated people. These ecosystems are a source of food and water, medicine, clean air, materials to build houses, and inspiration and awe. For city people, tropical forests often represent the unknown and sources of threatening diseases and dangerous animals. They also represent one of the last frontiers for science as the interiors of some forests remain largely scientifically unexplored (e.g., Lomami Forest in the Democratic Republic of Congo, DRC; Nouabale-Ndoki in the Republic of Congo; Manu, Peru; Roraima Forest and Cordilleras in Venezuela and Guiana; Papua-New Guinea tropical forests). New species of animals and plants are being discovered in tropical forests every year. In a well-known study, Erwin (1988) demonstrated that we know only a small portion of the invertebrates of a Neotropical forest, especially those living in the canopy, and calculated that there is between 10 and 30 million species of plants and animals on Earth. This estimate was later reduced to 8 million species, but still the majority will be found in tropical forests (Mora et al., 2011). One research area that can provide information critically needed for conservation is movement ecology. However, studying movement ecology in tropical forests is often logistically very difficult. Therefore, it is not surprising that we know little about the movement of tropical forest species compared to those living in open areas.

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1.1 Introduction to Tropical Forest Mammal Studies

Tropical forests have long fascinated people. These ecosystems are a source of food and water, medicine, clean air, materials to build houses, and inspiration and awe. For city people, tropical forests often represent the unknown and sources of threatening diseases and dangerous animals. They also represent one of the last frontiers for science as the interiors of some forests remain largely scientifically unexplored (e.g., Lomami Forest in the Democratic Republic of Congo, DRC; Nouabale-Ndoki in the Republic of Congo; Manu, Peru; Roraima Forest and Cordilleras in Venezuela and Guiana; Papua-New Guinea tropical forests). New species of animals and plants are being discovered in tropical forests every year. In a well-known study, Erwin (1988) demonstrated that we know only a small portion of the invertebrates of a Neotropical forest, especially those living in the canopy, and calculated that there is between 10 and 30 million species of plants and animals on Earth. This estimate was later reduced to 8 million species, but still the majority will be found in tropical forests (Mora et al., 2011).

Despite their ecological, economic, and scientific importance, tropical forests are being negatively impacted faster than any other biome on Earth. Globally, ~60 million ha of tropical primary forest were lost from 2002 to 2019 (Weisse & Gladman, 2020), and 21% of this loss occurred in Africa (Estrada et al., 2020; Chapman & Peres, 2021). Thus, ecological research that can be used to protect these ecosystems are critically needed.

One research area that can provide information critically needed for conservation is movement ecology. This field was recently launched as a new paradigm (Nathan, 2008). It was framed as a discipline of ecology that investigates the causes and consequences of animal movement. Traditionally animal movement was studied in narrow ways from several separate scientific disciplines; however, Nathan et al. (2008) argued that what was needed was a paradigm that integrated several disciplines, including locomotion abilities, neurocognitive abilities, internal states, external conditions, and the animal's ecology.

However, studying movement ecology in tropical forests is often logistically very difficult. In savanna systems, researchers can often observe animals from far distances, often from the comfort and safety of a vehicle; this is simply not possible in a dense tropical forest. Furthermore, many of tropical forest species are shy and avoid approaching observers, and they can be rare and difficult to encounter. Using technological advances in drones, telemetry, and camera trapping (Kays et al., 2015; Chapman et al., [this volume](#), Chap. 11) has allowed advancement in movement ecology of tropical forest mammals. However, capturing animals to deploy collars is difficult and dangerous (see Chap. 2 this book, Reyna-Hurtado et al., [this volume-a](#), Chap. 2), and the humid environment of the forest means the longevity of devices is often much reduced (Reyna-Hurtado et al., 2016). Therefore, it is not surprising that we know little about the movement of tropical forest species compared to those living in open areas.

1.2 African Tropical Forest Studies

The study of African tropical animals has occurred in relatively few sites. Some have become long-term study sites. For example, at Nouabale-Ndoki, the study of forest elephants (*Loxodonta cyclotis*), lowland gorillas (*Gorilla gorilla*), buffalos (*Syncerus caffer*), and bongos (*Tragelaphus eurycerus*) has been possible since observations can be made at a bai where animals come to feed on mineral-rich soils (Korte et al., [this volume](#), Chap. 5; Blake & Maisels, [this volume](#), Chap. 3). Several of sites were established by primatologist including the Gombe National Park in Tanzania (Goodall, 1986), Virunga National Park in DRC (Fossey & Harcourt, 1977), Parc of Volcanoes in Rwanda (Fossey & Harcourt, 1977), Kibale National Park in Uganda (Struhsaker, 1975; Wrangham et al., 1991; Chapman et al., 1995), Tai Forest in Ivory Coast (Boesch & Boesch-Achermann, 2000), and Wamba in DRC (Kano, 1982). These long-term efforts facilitated a great deal of primates and non-primate research as they provided much needed logistical support.

However, despite these efforts, there are still many species that we know very little about. For example, despite considerable effort, we were unable to find authors who could contribute a chapter to our book on forest carnivores or on some common, range-wide species such as red river hogs, duikers, or other antelopes.

In 2019, we (Reyna-Hurtado & Chapman, 2019) brought together a series of studies on animal movement in Neotropical forests, and now in 2023, we are replicating this effort but with studies from Afrotropical forests. We hope these volumes stimulate more research on animal movement inside the fascinating, but fragile, tropical forests of the world and point to gaps in knowledge. In the next sections, we summarize the chapters of this book, and we suggest possible new directions for the study of animal movement in tropical environments.

1.3 Book Presentation

This book presents 11 chapters on the movement ecology of several mammal species found in the tropical forests of Africa.

In Chap. 1, Reyna-Hurtado, Chapman, and Melletti introduce the chapters and summarize a state of the knowledge of movement ecology for Afrotropical forest mammals and suggest new directions to design studies on movement ecology for mammals living inside Africa tropical forest.

In Chap. 2, Reyna-Hurtado and collaborators present the first documented home range estimates for a group of giant forest hog (*Hylochoerus meinertzhageni*). This is one of the largest suids in the world and is an endangered species that, despite a wide distribution, is surviving in just a few protected areas. The study was done in Kibale National Park in Uganda over 5 years. The fact that giant forest hogs live in dense tropical forest, is shy, and is targeted by poachers made the study of this population extremely difficult. The authors present home range estimates (four

methods), occupancy rate, detection probability, and daily movement patterns. They also provide ecological and behavioral information on group sizes, group structure, and feeding habits.

In Chap. 3, Blake and Maisels analyze the movement of forest elephants (*Loxodonta cyclotis*) and consider driver movements. They found that movement was strongly influenced by a human-induced landscape of fear. They argue that large animals modify ecosystems at a scale larger than many protected areas. As a result, conserving forest elephants will require multicountry efforts to manage tropical forests across country borders.

In Chap. 4, Reyna-Hurtado and colleagues present a multiyear analysis of elephant family groups in Kibale National Park, Uganda. Using camera traps set at water sources and mineral-rich sites, they provide information on visitation rate, occupancy rate, detection probability, index of relative abundances, and movement patterns. They also describe the time elephant's family groups visit water sources and if these visits are related with crop raiding activities outside the park. Some behavioral data were obtained, such as family group size and visitation patterns (i.e., who arrives at water sources first and who leaves last). Understanding forest-living elephant movement is crucial to minimize conflicts between elephants and farmers and to understand the dynamics between elephant herd movements and forest dynamics.

In Chap. 5, Korte et al. present an analysis of forest buffalos (*Syncerus caffer nanus*) for a Congo Basin tropical forest. They highlight that compared to the well-studied savanna buffalo (*S.c. caffer*, *S.c. brachyceros*, *S.c. aequinoctialis*), there is little information on forest buffalo. Their research reveals that compared to savanna buffalo, forest buffalo have smaller home ranges, shorter daily movement, no seasonal movement, and smaller group sizes. Korte et al. also suggest that genetic health is an important parameter to take into consideration when developing management practices and suggest that establishing wildlife corridors that allow gene flow between isolated populations may be critical for the future of forest buffalo populations.

In Chap. 6, Kalbitzer and collaborators examined 10 years of data on the leaf-eating (and endangered) red colobus (*Piliocolobus tephrosceles*) in Kibale National Park, Uganda. Using the most updated method to estimate home range (autocorrelated kernel density estimator), they evaluated if home ranges changed over the years. They found that red colobus shows high fidelity over the 10 years. The authors explore the relationship between site fidelity and type of food consumption.

In Chap. 7, Thureau and collaborators reviewed the movement patterns in primates across Africa tropical forest and food acquisition. They argue that to find suitable food, animals must navigate through a matrix of resources that vary in their concentrations of nutrients, toxins, and digestion inhibitors while also avoiding multiple hazards, such as food competitors and predators. Thureau et al. reviewed the movement ecologies of primates in African forests with a focus on nutrient acquisition. They discuss how primates find different nutrients using a variety of sensory adaptations and adapt their movements to meet specific nutritional needs.

In Chap. 8, Bonnell and collaborators provide a theoretical contribution where they introduce the “landscape of fear from diseases” as a driver of animal movement. This original chapter argues that similar to when predation attempts create learned associations between landscape features and predation risk, disease could have similar effects and influence movement. In this chapter, Bonnell et al. examine evidence of a “landscape of fear from disease,” which is when individuals show avoidance or increased vigilance of disease threats in specific locations. The authors present a framework that identifies elements responsible for the development of a landscape of fear from disease. They then use this framework to pinpoint combinations of pathogen characteristics and host movement behaviors that are likely to facilitate learned associations between landscapes and disease threats. Some of these combinations are likely to occur in the context of African forest mammals and thus influence their conservation.

In Chap. 9, Robira et al. present a study of what drives group movement in western gorillas (*Gorilla gorilla*) of the Central African Republic. They compile published and new evidence to investigating how the seasonal frugivorous western gorillas decide where to feed (movement heuristic and spatial knowledge), how to go (e.g., movement speed and straightness), and when to go (temporal knowledge) and come back to feeding sites (recursion pattern) to shed light on the foraging strategies and the underpinning cognition in response to their diet seasonal changes (high and low fruit seasons). Robira et al. found that western gorillas rely on spatio-temporal knowledge to decide where to go and when in both seasons. They argue that understanding mechanisms affecting animal foraging efficiency is crucial in the current context of global climate changes and its unpredictable consequences on food availability.

In Chap. 10, Hongo Shun examined movements of mandrills (*Mandrillus sphinx*), an endangered species of primate that has received little scientific attention. This species has an unusual social system for a primate forming huge groups of hundreds of individuals, with males moving in and out of the group seasonally. Shun summarizes what is known about how groups remain in contact and how solitary adults rejoin groups. Group crowdedness and frequent exchange of long-distance calls are key to the collective movement of large groups that engage in regular subgrouping. The adaptive benefits of the large group size possibly lie in female tactics relating to infanticide avoidance and polyandrous mating. While very little is known about how solitary males find groups at the onset of the mating season, their seasonal influxes can be relatively well explained as foraging and mating tactics. Since the major questions of mandrill social organization are strongly related to their movement ecology, the intensive research of movement and positioning behavior using GPS telemetries and remote sensing is crucially needed to disentangle the social system of this intriguing monkey.

Finally, in Chap. 11, Chapman, Reyna-Hurtado, and Melletti link movement ecology with conservation biology, and with clear examples, they make the case that conservation actions will benefit from information obtained within the framework of movement ecology. Chapman et al. summarizes the goal of this book – the need for scientific information that enriches conservation decision-making.