

Chimpanzee

The chimpanzee is one of our planet's best-loved and most instantly recognizable animals. Splitting from the human lineage between four and six million years ago, it is (along with its cousin, the bonobo) our closest living relative, sharing around 99 percent of our genes. First encountered by Westerners in the seventeenth century, virtually nothing was known about chimpanzees in their natural environment until 1960, when Jane Goodall traveled to Gombe to live and work with them.

Accessibly written, yet fully referenced and uncompromising in its accuracy and comprehensiveness, this book encapsulates everything we currently know about chimpanzees: from their discovery and why we study them to their anatomy, physiology, genetics, and culture. The text is beautifully illustrated and infused with examples and anecdotes drawn from the author's 30 years of primate observation, making this a perfect resource for students of biological anthropology and primatology as well as non-specialists interested in chimpanzees.

Kevin D. Hunt is Professor of Anthropology and an affiliate of the Stone Age Institute at Indiana University, Bloomington. He is also Founder and Director of the Semliki Chimpanzee Project, which was established in 1996 to study and preserve the chimpanzees in the Toro-Semliki Wildlife Reserve. Broadly trained in various anthropological disciplines, much of Professor Hunt's published work has centered on functional morphology and what chimpanzee locomotion, posture, and ecology can tell us about what led humans to diverge from apes and what advantage bipedalism gave our chimpanzee-like ancestors roughly five million years ago.

“Chimpanzee: Lessons From Our Sister Species

condenses over 60 years of chimpanzee research into an informative and entertaining book. Drawing on his own first-hand experience, the research of other scientists and historic accounts, Kevin Hunt describes the fascinating lives of chimpanzees in the wild, as well as the research methods used by leading experts in the field. If you want to know just how alike we truly are to our closest living relatives then you will get a very good idea from reading this book.”

Jane Goodall, PhD, DBE, Founder of the Jane Goodall Institute & UN Messenger of Peace

“Hunt skillfully weaves anecdotes and history into this scientific compendium of the behavioral ecology, biology, and evolution of chimpanzees. The book is generously illustrated, and each chapter includes extensive references. It is written in an accessible, conversational style that could only be achieved by someone with Hunt’s first-hand experiences in the field and encyclopedic perspective. It will make a valuable reference for anyone interested in what is known and not yet known about one of our closest living relatives.”

Karen B. Strier, Vilas Research Professor & Irven DeVore Professor, Department of Anthropology, University of Wisconsin-Madison, USA

“An exceptional book that delivers on every promise in its table of contents. Grounded in Hunt’s 30+ years of chimpanzee field work and his commanding knowledge of others’ research, he gives us a state-of-the-art research volume that will become an essential reference for primatologists, and anyone who wants to understand the true nature of our sister species.

Hunt’s writing is lucid, scholarly and wide-ranging as he carefully explains chimpanzee evolution, biology, social behavior, and so much more. Hunt skillfully embeds his own field observations to help readers grasp concepts like chimpanzee positional behavior, personality, maternal behavior, cognition and communication, hunting and aggression. He balances this perspective with a wealth of laboratory and captive findings.

The extensive references for each chapter provide an outstanding resource for students, teachers and readers who choose to delve further. The volume is generously illustrated with photos, line drawings and abundant figures that enrich the text.”

Linda F. Marchant, Professor Emerita, Miami University, Oxford, Ohio, USA

Chimpanzee

Lessons from our Sister Species

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To Marion
the sine qua non

*Half the author's profits from this book
will be donated to chimpanzee research
www.indiana.edu/~semliki*

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FOREWORD

In every society, for as long as we have had records, people have grappled with the great existential question. Why are we here?

In 1859, Charles Darwin published *On the Origin of Species*, and the theory of evolution by natural selection was born. Within a century, biologists were increasingly confident that a single evolutionary tree linked all life on Earth. The exciting questions then became how to explain the evolution of particular species and their characteristics – even humans.

Humans proved to have evolved from a forest-living African ape living some seven million years ago. That ancestor was closely related to gorillas, and it spawned two lines. One led to the chimpanzees (including bonobos, also known as pygmy chimpanzees); the other led to us.

Chimpanzees had long been of interest, but in the second half of the twentieth century two scientific leaps made these apes especially fascinating. The advances happened independently of each other. They were both thoroughly unexpected.

First was a series of reports from Jane Goodall and Toshisada Nishida that chimpanzees in Tanzania practice various behaviors that had been thought of as markers of humanity. The apes modify objects into tools that they use to help get their food. They hunt for fresh meat and share the kill with each other. Males conduct raids into neighboring territories, where they stalk and kill lone victims. And gestures and facial expressions used by chimpanzees can be so similar to those used by humans – such as an outstretched hand and an intense stare when begging – that many are intuitively understandable. In short, chimpanzees are unnervingly human-like in the wild. They prove to share more behaviors with us than does any other wild species.

Second was the discovery that chimpanzees are more closely related to humans than they are to gorillas. The idea was at first so startling that many people did not believe it. The skepticism is easily understood: Chimpanzees look so like gorillas that

they are easily confused with them. So, naturally enough, the traditional assumption was that chimpanzees' closest relatives were gorillas. But eventually the genetic data became overwhelming. Humans really are genetically closer to chimpanzees than are any other species, even gorillas.

What does it mean that chimpanzees behave more like us, and are also more closely related to us, than to any other species? *Chimpanzee* answers that question by giving a rich account of the evolution of both chimpanzees and humans.

To do so, Hunt examines the relationship between ape and human from a broader perspective than any book has done. His eclectic approach takes courage. To succeed as a scientist, one needs to be an expert on a narrow slice of the natural world. So it is easy (and safe) to forget the big picture. But Kevin Hunt has bucked the trend by going beyond his background as a functional morphologist. He treats the natural history of these apes like a detective story, following leads wherever they happen to take him.

His quest begins with problems arising from his own initial fieldwork. He observed individual chimpanzees at close quarters for a year. He saw their social lives giving way to the search for food, especially the daily need to find scarce patches of freshly ripe tree-fruits as places for morning meals. That observation provoked questions that Hunt follows up. What aspects of digestive physiology commit the apes to a diet of tree-fruits? What does that commitment mean for their anatomy? Why do they differ from humans in these ways? The answers to such questions took him into many corners of evolutionary biology. Eventually he combined them into a big, satisfying picture of the species' adaptations to its environments.

Chimpanzee's far-reaching perspective embraces other species, too. Hunt's book is mostly about the more widespread species of chimpanzee, which is known simply as "the chimpanzee." It lives in some 20 countries on the northern, right-hand bank of the

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Congo, including Tanzania and Uganda, where Hunt has done his major fieldwork. But Hunt also writes about the other species of chimpanzee, the bonobo. Bonobos live on the southern, left-hand bank in a much smaller geographical range, entirely within the Democratic Republic of the Congo. Their differences from their sister species provide many new evolutionary problems to consider.

So, too, do the apes of the past. *Chimpanzee* ventures back in time as well, exploring the biology and adaptations of the australopithecine apes that dominated the evolutionary history of the pre-human lineage from around seven million to two million years ago.

Ever since the seventeenth century, when chimpanzees were first brought to Europe, writers have suspected that apes have a story to tell about human life and our prehistoric origins. Year by year the details of that story are being worked out better and better. *Chimpanzee* is a terrific account from the leading edge.

Richard Wrangham

*Ruth Moore Research Professor of Biological
Anthropology, Department of Human
Evolutionary Biology
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PREFACE

The history of chimpanzee scholarship has been one of generally gradual but occasionally sudden shifts in the perception of how closely related humans and chimpanzees are. Here I will try to bend that perspective a little bit to view chimpanzees more as a counterpoint to human uniqueness, taking care to point out how they differ from humans and how explaining those differences helps us to understand human evolution, including our frailties and failings. To draw out those insights, I will attempt an unhurried grand tour through the natural sciences, always with chimpanzees in the forefront, always contrasting their biology and behavior to that of humans. I intend this volume to be current and thoroughly grounded in the latest research, only one step from formal scholarship, but at the same time stripped of the jargon-heavy phraseology that weighs down many similar efforts. Where I use obscure terms, I will attempt to define them on the fly.

I see my audience as scholars from other fields, laypersons with a sincere interest in the behavior, biology, and history of primates, doctoral students in human evolution, human biology, and primatology, and colleagues in scholarly specialties neighboring my own. If successful, it will be a volume worth dipping into for scholars in any natural science field, even the chimpanzee expert. I hope a primatologist might turn to this volume if he or she wants to dabble in functional anatomy or endocrinology. While I realize this is probably too much to hope for, I sought to make the book engaging enough that a colleague or student might be drawn into exploring an area they had not anticipated investigating. Ideally, this volume would be an accessible version of the six-volume G.H. Bourne volume *The Chimpanzee*, published from 1969 to 1973.

As I worked, I found that sometimes the most thorough investigation of a subject – for example, balance, hearing, ape cognition, aspects of gross anatomy – is half a century old. In the course of discovering the chimpanzee, researchers sometimes

got it right the very first time, in which case I cited the classic scholarship that shaped a particular issue, occasionally skipping a recent publication that added a minor flourish to the subject. I would like this volume to be something of the corrective to the tendency I have seen recently among younger scholars to cite the most recent publication on some subject, no matter how tangential, ignoring truly foundational work with which they ought to be familiar. Other times experts long labored under misapprehensions that have been corrected only recently, in which case I focused on the recent scholarship with only a nod to ancient errors. My shorthand way of summarizing my emphasis on studying micro- and macrobiology, as well as behavior, is that while the bricks are indeed interesting, they are most interesting when they help us understand the castle.

I began this project in a small way in 1996, when I had just begun to teach a class at Indiana that – in a modest way – surveyed the breadth of chimpanzee research. I called it *Sister Species: Lessons from the Chimpanzee*. The text for the class was a coursepack made up of review articles and a few specialist research articles. The readings that were most successful with students, I learned from student evaluations, were often those from *Evolutionary Anthropology*. These were professional-grade offerings, current and cite-able, but still accessible to committed neophytes. I have tried to work on that model in this book.

The first few times I taught *Sister Species*, the first reading in my coursepack was a brilliantly written news article by Claire Martin (1994), a short work that focused on chimpanzee and human cognitive similarities. Students loved it. As evocative as this work was, I was left feeling that the reading for my first lecture should have a slightly broader perspective and more robust scholarly citations. That same year, 1996, I started research on chimpanzees at the Toro-Semliki Wildlife Reserve, Uganda. One day, problems

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with my vehicle left me stuck in a chimpanzee-less part of the reserve for two hot, humid days with nothing to do but sweat. During this time, I wrote a short exposition that quoted extensively from Martin's article but went on to cover a broader constellation of ideas that I hoped would best set the stage for my first lecture. It would have done its job well except that almost as soon as I finished it the intense heat fried my hard drive. I lost everything but a couple of paragraphs I had copied onto a floppy disk.

Anyone who has lost a piece of work like this knows how disheartening it can be, and how the virtuosity of the lost work swells in the imagination, discouraging a rewrite. Although I still had the framework in my head, it was almost 10 years before I rewrote that chapter. When I brought the finished work to students they welcomed it enthusiastically, encouraging me to write a few more chapters to fill gaps in my reading list. As I wrote those short chapters I began to piece together plans for this volume. I aimed to review chimpanzee functional anatomy research (which it will be apparent I revel in) in such a way that my colleagues who specialize in social behavior might be tempted to look into it for links to their own work; for instance, I hoped my review might allow primate paleontologists to think more deeply about the role social behavior plays in anatomical evolution. And *vice versa*. I blocked out the table of contents in 2005 during a delightful sabbatical at the Max Planck Institute in Leipzig, during which time I emerged with 4 of the 30 chapters, enough to get a book contract. I only got serious about writing after signing a contract in 2013.

As I completed parts of the manuscript, I occasionally passed on a chapter to a "civilian," a friend or colleague who had no background in primatology. Their responses were encouraging enough that it was brought home to me in a way it had not been before that chimpanzees are charismatic enough to serve as a sort of hook or ice-breaker that might rather painlessly introduce the breadth of natural science to new audiences. As I wrote subsequent chapters I found myself adding a flourish here and an elaboration there that I felt gave a narrative boost to the "story," leavening the stultified

scientific language that always threatens to smother scholarly writing. I hoped that a personal anecdote or amusing fact here and there might make wading through the more painstaking scholarly concepts easier and more rewarding.

Buried in each chapter are a few original insights that I hope someone will latch onto and expand upon, but which, regretfully, are not very likely to reach specialists in that area, who are naturally unlikely to pick up a survey book like this. I hope advanced students who happen upon this volume will recognize those original and informed speculations, which I have summarized in Appendix 2, and carry them to their doctoral supervisors as possible research or dissertation topics.

As we embark on this journey, let me offer, at the suggestion of one of my editors, a few personal details. I am a third-generation Gombe researcher, though not a typical one. My doctoral and postdoctoral supervisor was Richard W. Wrangham, a name that will appear many times in the pages to follow. He came to Gombe in 1974 and became the first researcher to make the all-day, 13-hour, nest-to-nest follow the foundation of his research. It was through his encouragement that I backed into chimpanzee research, but not before trying to avoid it. I may hold the distinction of being the most reluctant beneficiary of the research world Jane Goodall inspired at Gombe and Toshisada Nishida at Mahale. My research is focused on the evolution of bipedalism, and I began my doctoral work just as a reassessment of the *Lucy Australopithecus afarensis* fossils was underway. Early on, australopith publications by paleontologists Donald Johanson and colleagues emphasized the human-like morphology of Lucy, particularly her very human – though not completely human – pelvis and lower limb (Johanson & Taieb, 1976; White et al., 1981). Further evidence that australopiths were human-like came from tooth development research that suggested early hominins had a long, human-like juvenile period (we call this a "slow life history"), perhaps an indication of advanced cognitive abilities.

This "miniature human" or homunculus hypothesis, as some derisively referred to it, was soon challenged. With more fossils to work with, B. Holly Smith found

that the rate of maturation of australopiths was chimpanzee- rather than human-like, and not just a little like chimpanzees, but much more ape-like than human-like (Smith, 1987). Two landmark articles reassessed Lucy's anatomy, one by anatomists and paleontologists Jack Stern and Randy Susman (Stern & Susman, 1983) and a second by French paleontologists Brigitte Senut and Christine Tardieu (Senut & Tardieu, 1985). These showed that while Lucy and other members of her species had human-like hips and legs, they also exhibited arboreal anatomy wherever it might not interfere with upright walking – australopiths have long toes, short legs, and flexible joints, for instance. Above the waist, australopiths were far more chimpanzee- than human-like. As a shorthand, their studies suggested that australopiths are better described as heavy-faced chimpanzees from the waist up and human-like from the waist down.

But even if the anatomy of Lucy is ape-like, what does that mean? It turned out that we had not yet gathered quantitative information on locomotion and posture in chimpanzees that could link a particular anatomical detail, a cone-shaped thorax, for instance, with a behavior. Yes, Lucy's ribcage, **robust** (this term will come up again and again: "heavily built") fingers, elbows, and toes were chimpanzee-like, but what did that mean for her behavior? Did australopiths live in the trees? Were these traits linked to climbing, hanging by an arm, walking on the ground, or what? We did not know, because we had little data on chimpanzee locomotion. Knowing what chimpanzees used their unusual anatomy for was critical – presumably Lucy used her body the same way. But chimpanzees hold another key. Did chimpanzees ever stand up like humans, and if so what motivated them to stand? Both bits of information would help us understand first how Lucy lived and, extrapolating, from that information, why humans evolved bipedalism.

I approached Richard Wrangham to see if I could mine these data from his records. If not, could we talk someone at Gombe into making some notes on chimpanzee locomotion? Richard realized from the beginning this make-do plan was half-baked. With no idea how much effort it required to accomplish it, or

how much it would affect my scholarly life, I mulled over his exhortations that I should gather this information firsthand. When I finally agreed, after an idiotically long time considering it, he arranged with the late Toshisada Nishida and Jane Goodall for me to work at these two world-famous study sites. I will be forever grateful to this trio.

When I began watching chimpanzees I quickly realized, as I should have beforehand, that their dietary needs were behind much of their minute-to-minute movements. I had to pay attention to their food to understand their locomotion and posture. Access to the best feeding sites seemed to be related to social rank and sex. High-ranking males moved differently than low-ranking males, and females differently as well, so that I had to understand their social relationships to fully understand their locomotion. Their social relationships were grounded in larger societal issues like territorial defense. I found myself being sucked ever deeper into the study of the social world of chimpanzees and I came to understand the force of John Muir's famous quotation: "when we try to pick out anything by itself, we find it hitched to everything else in the Universe." Following Wrangham's lead, I began to interest myself in things like food chemistry and male violence. I found Goodall's work on the challenges of mothering and the evolution of advanced cognition to be more interesting. While I started my chimpanzee research only interested in what it could tell me about fossils and the evolution of bipedalism, after working at Gombe and Mahale I found these other issues every bit as exciting. I moved on to a postdoctoral fellowship with Wrangham and helped his team gather data for his pioneering work on food chemistry and ape and monkey adaptations (Wrangham et al., 1998), an area of interest I have continued to pursue (Hunt, 2016).

As I worked in a two-year postdoc position with Wrangham, I applied for a job at Indiana University, an unusual job that seemed well-suited to me. In what I have come to know as typical Indiana frugality, the university balked at hiring both a primatologist and a human paleontologist and sought to cram two or three jobs into one – at Harvard, where I had been a postdoctoral fellow, there had been three professors and two other staff in these two fields. I accepted the

position at Indiana and thus began a very atypical teaching career that spanned primatology and human paleontology. With this somewhat forced diversification, I found myself free to pursue my interest in virtually every aspect of chimpanzee research. As I taught human paleontology and primate social behavior year after year, and as I continued research on wild chimpanzees, I thought

more than I might have otherwise about what lessons chimpanzees can teach us about human evolution, what our place is in this world, and what it means to be human; and to be chimpanzee.

While I may have come to chimpanzee fieldwork reluctantly, it has become my life's work. As you enter the fascinating world of chimpanzees, you may see why. *Pan in sempiternum!*

References

- Hunt KD (2016) Why are there apes? Evidence for the co-evolution of ape and monkey ecomorphology. *J Anatomy* 228, 630–685.
- Johanson DC, Taieb M (1976) Plio-Pleistocene hominid discoveries in Hadar, Ethiopia. *Nature* 260, 293–297.
- Martin C (1994) A question of humanity. *Denver Post Magazine*, 18 December, p. 12.
- Senut B, Tardieu C (1985) Functional aspects of Plio-Pleistocene hominid limb bones: implications for taxonomy and phylogeny. In *Ancestors: The Hard Evidence* (ed. Delson E), pp. 193–201. New York: Alan R. Liss.
- Smith BH (1987) Maturational patterns in early hominids. *Nature* 328, 673–675.
- Stern JT, Jr, Susman RL (1983) The locomotor anatomy of *Australopithecus afarensis*. *Am J Phys Anthropol* 60, 279–317.
- White TD, Johanson DC, Kimbel WH (1981) *Australopithecus africanus*: its phyletic position reconsidered. *S Afr J Sci* 77, 445–470.
- Wrangham RW, Conklin-Brittain NL, Hunt KD (1998) Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance: I. Antifeedants. *Int J Primatol* 19, 949–970.

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In addition to welcoming me to Kibale-Kanyawara and hiring me into my first professional academic job, Richard introduced me to primatology and shared with me many anecdotes, ruminations, and speculations on primate evolution that I treasure. Our lively discussions taught me as much about chimpanzees and primates as his brilliant lecturing. The influence of his scholarship will be evident in nearly every chapter of this volume.

After Richard, Loring Brace had the most profound influence on my scholarly worldview, and his perspective – one that values history, logical, consistency and attention to detail – strongly influenced this work, particularly the discussion of fossils and the evolution of bipedalism. With Richard, he co-supervised my doctoral education. More important than the details of fossils, his dynamic perspective on the forces of evolution and his brilliant historical vision inspired me.

Three scholars at my home institution, Indiana University, cooked up the idea of hiring some young scholar into a position where his or her teaching responsibility would combine primatology and paleontology. It was this unconventional pairing that allowed me to keep a foot in each field over my career. I am grateful to Della C. Cook, Paul L. Jamison, and Robert J. Meier. Once at IU, I was quickly drawn into the orbit of paleoanthropologists Kathy D. Schick and Nicholas P. Toth, both of whom have influenced and encouraged my scholarship since my first days in Bloomington.

Of course, none of this would have mattered without the early mentorship of my undergraduate advisor, Fred Smith. Somehow, he put up with my numerous sophomoric (in this case, quite literally) shenanigans and pushed me along to a fulfilling (and published) Honors thesis and then into a graduate career. I flatter myself that he and I think alike, and his scholarship on Neanderthals and adaptation, in particular, have strongly influenced me.

Every scholar finds a few colleagues with whom he can have the sorts of conversations that flow easily and push ideas forward in such a contagious way that insights pile up far out of proportion to the time spent in discussions. For me, Lucia Allen, Bill McGrew, Blaine Morgan, Esteban Sarmiento, Tom Schoenemann, and Susannah K.S. Thorpe have been such collaborators. I thank them.

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This volume is the lineal descendent of five similar works. It will be apparent to any astute reader that Goodall's *Chimpanzee of Gombe* was a crucial resource and inspiration, in both organization and content. Her chapters on foraging, diet, cognition, tool use, and society were particularly foundational. Yerkes and Yerkes' (1929) *The Great Apes: A Study of Anthropoid Life* was the source that first introduced me to a historical perspective on chimpanzee scholarship, and my history chapter relies on it and Vernon Reynolds' *The Apes*, as well. Adolf Schulz's scholarship, particularly *The Life of Primates*, was a powerful influence on my understanding of primate biology. His brilliant illustrations are sometimes reproduced here, but influenced my approach to many of my original images as well. G.H. Bourne's *The Chimpanzee* filled in important gaps and its comprehensiveness influenced early planning.

The work of my excellent editors at Cambridge University Press was made much less onerous by the unexpected and therefore all the more appreciated editing of Debra Pekin. She made time to read the entire manuscript and helped not only with grammar, spelling, and style, but also big-picture tasks like consistency, tone, transitions, and accessibility. She helped me find the right places to remind readers of the purpose of the volume. Thank you, Deb. My daughter, M. Alison Hunt, is an accomplished editor who is somehow able to find that perfect word to express my intent better than I did; several chapters benefited from her expertise.

Given the breadth I have aspired to here, some chapters relied heavily on one or two pieces of scholarship, particularly large, comprehensive reviews, or on comments and editing by only one or two colleagues. I must mention some of them here.

Chapter 1 was inspired by a wonderful article on human-reared chimpanzees by Claire Martin, a work I still reread over 20 years later. Alyce Miller helped to focus the chapter more cleanly. Harry Raven's 1932 and 1933 articles on Meshie provided the foundation for the chapter (see individual chapters for the references).

The works of C.R. Carpenter (1942), Irv DeVore (1965), and the massive *Primate Societies* (Smuts et al., 1986) were important resources for Chapter 2, updated of course with more recent offerings. That said, when McGrew's 2016 review of chimpanzee field studies appeared I incorporated important ideas from it.

Chapter 3, on the history of chimpanzee science, has at its foundation Yerkes & Yerkes (1929), Hill (1969), Reynolds (1967), and Goodall (1986). Dale Peterson read this chapter early on and saved me from several mistakes and errors of emphasis. Decades of interaction with Loring Brace sharpened my appreciation of the importance of historical depth when attempting to understand any scholarly area, and his views on the Great Chain of Being and the influence of European colonialism on the discovery of the chimpanzee are apparent.

I am grateful to the late Colin Groves for patiently answering questions about taxonomy that vastly improved Chapter 4 and the taxonomy appendix. Betty Rose Nagle, a Professor Emerita of Classical Studies here at IU, helped me with some of the Latin inherent in taxonomy.

R.W. Wrangham's enormous body of scholarly work on primate diets, nutrition, foraging, and plant chemistry inform Chapters 5 and 6 – those that cover diet, habitat, and digestion. Alain Houle and I had several conversations about these chapters and his advice improved them. John Mitani and especially Nick Newton-Fisher helped compile information on diet for Chapter 5. Almost all of the information on tropical forests in this chapter was based on T.C. Whitmore's stylish and informative *Introduction to*

Tropical Forests. Chapter 6 owes much to David Southgate's wonderful 1995 digestion review, but also to work by Chivers, Givannoni, Gautier-Hion, Hladik, Lambert, Milton, and Wrangham. Jim Giovannoni read and improved the section on fruit ripening.

Chapters 7, 8, and 9 on anatomy, functional morphology, locomotion, and posture are the focus of my own scholarship, but my understanding of these topics grew out of study of the works of Charles Oxnard and publications by and conversations with Mary Marzke, John Fleagle, John Cant, Rich Kay, Bill Jungers, Esteban Sarmiento, and Mike Rose. Kris Carlson and I engaged in many thought-provoking discussions of function and form both during his days as my graduate student and since. David Pettifer commented helpfully on all three of these chapters while swatting tsetse flies in the sweltering heat of Semliki.

Some of Chapter 10 started out as a grant proposal I wrote with Kelly Baute. Other parts began as an article I published in 2016. Susannah K.S. Thorpe commented on early versions the chapter. As it took a more final shape, Jay Kelley meticulously ferreted out errors of fact, emphasis, grammar, and terminology, and shared with me his different perspective on ape and monkey competitive relationships, or the lack thereof. He and I exchanged enough word-volume via email to make a short book. I am very grateful. I treasure colleagues who can engage in spirited debates without rancor and with collegiality even when there are fundamental differences in outlook, and Jay is one of those colleagues. However, he failed to convince me of the primate paleontological community's certainty that *Proconsul/Ekembo* is merely a stem hominoid, only indirectly related to living apes; I take the more liberal view that if not *Proconsul*, something very like it and closely related to it was at the root of the ape lineage. He takes a more conservative perspective on chimpanzee and OWM competitive relationships and on any number of small details where I went out on a limb, if you can excuse the pun. He should not be blamed for my divergent viewpoint.

Chapter 11, on growth and development, drew heavily on Adolf Schultz's work and Paul Jamison's as well; Paul edited the chapter. Shawn Hurst edited

and commented as well, and helped with the brain figure. My summary of evo-devo and homeobox genes depended mostly on Sean Carroll's excellent book on the topic; the late Rudy Raff commented helpfully and his wonderful *The Shape of Life* helped immensely.

Robert J. Meier very kindly edited Chapter 12 and John F. McDonald commented on apoptosis. Randy Brutkiewicz and Yansheng Du helped me understand the function of the *IL* gene family and interleukins.

Diana Kewley-Port patiently explained the physics of sound to me over drinks one afternoon at Yogi's Bar and Grill, which helped tremendously for Chapter 13 on the senses.

As with Chapter 10, some of Chapter 14 started out as a grant proposal I wrote with Kelly Baute. Sean Prall very kindly provided extensive and very helpful comments and edits on the entire chapter. Thank you, Sean.

The scholarly work of my valued former IU colleague, Michael Muehlenbein, and Michael's and Richard Bribiescas' review chapter (see Muehlenbein, 2015) served as the basis for Chapter 15 on hormones. Michael provided comments on Chapter 14 as well.

Jane Goodall and Anne Pusey founded chimpanzee mothering research, and Chapter 16 is packed with their insights. Katherine A. Cronin generously shared her wonderful photographs of a mourning mother with me.

Craig Stanford very graciously set aside time to comment on Chapter 17, my hunting review, even while he was simultaneously putting the finishing touches on a competing (drats!) volume.

Tom Schoenemann coached me through some of the intricacies of brain anatomy and helped with Chapter 19, on the mind, as well.

Shawn Hurst reviewed Chapters 18 and 19 and provided some of the figures. More importantly, his interest in the brain as he blocked out his dissertation research inspired me to learn more about it. His lively imagination and thoughtful perspective on the mind and brain strongly influenced the chapter. Linda Marchant and I have had many discussions about handedness/laterality, tool use, and primate brains and I benefited enormously from her perspective. Colin Allen worked through the entire chapter on the

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mind, added important insights, and pointed out some glaring omissions. Discussions with Shawn, Tom Schoenemann, Peter Todd, Kathy Schick, Nick Toth, Sally Boysen, and Ralph Holloway were also extremely helpful and clarified many of the critical issues in these chapters.

Chapter 20 on sleep draws heavily on my former doctoral student David Samson's pioneering research and historical perspective, not to mention our many lively discussions about sleep and its evolution. He edited the chapter from top to bottom and improved it enormously.

Numerous discussions with Steve Franks and Tom Schoenemann sharpened my perspective on chimpanzee language, presented in Chapter 21. Steve made several editing passes at the chapter and helped me to understand the linguistic perspective on the evolution of language, one a little different from my own. Phil LeSourd's comments and advice added some nuance to the chapter. Tom Van Cantfort saved me from an embarrassing error and helped to form my writing on Washoe and research surrounding her. Mary Lee Jensvold shared her most recent research findings with me and helped to refine the chapter.

Chapter 22 is mostly a condensed and updated version of Bill McGrew's *Chimpanzee Material Culture*. His influence and research can be seen throughout this chapter and indeed throughout the entire volume. I wish I could write as clearly as he does. He generously edited the chapter adding important facts and perspectives, saving me from a number of embarrassing mistakes.

Chapters 23 and 24 are based on numerous conversations with Richard Wrangham and on Goodall's foundational work. Bill McGrew has been interested in chimpanzee culture for decades and his work is much cited as well.

Chapter 24 owes a great debt to Martin Muller's 2002 chapter on aggression as well as the work of Mike Wilson and Richard Wrangham.

Chapters 24, 25, and 26 grew out of the research and discussions with Richard Wrangham and fewer, though still valuable, back-and-forths with Bill McGrew.

Conversations with Tobias Deschner informed Chapter 27, and he generously supplied me with

images that help make sense of sex and reproduction in chimpanzees. My first exposure to reproductive endocrinology came when I worked with the late Pat Whitten as a teaching assistant in the 1980s. Thanks, Pat.

Chapter 28 is quite short considering that I have spent over 20 years working at Semliki and nearly three years actually on-site. I am grateful to the ownership and staff of the Semliki Safari Lodge. Jonathan Wright and his ecotourist company, WildPlaces, have provided support and collaboration for my research at Semliki from its beginning. Tim White graciously shared some of the images in the chapter. Many of my staff, employees of the Semliki Chimpanzee Project, have worked to sustain the project, but I am particularly grateful to the late Karamajong Kule, to Eriik Kasutama, and to former camp manager Moses Comeboy. I have benefited from the help of nearly three dozen assistant project managers – local supervisors – over the years. I cannot name them all, but some who were particularly indomitable, industrious, resilient, *and* faithful to their contracts (a six-month stint in a tent is no picnic) are Rachel Weiss, Jim Latham, Sacha Cleminson, Esther Bertram, James Fuller, Teague O'Mara, Chris Wade, Jim Reside, David Inglis, Jess Tombs, Carmen Vidal, Alissa Jordan, Tim Webster, David Samson, Maggie Hirschauer, Will Symes, Jeremy Borniger, Corey Mitchell, Caro Deimel, Luke Loudon, Katie Gerstner, Ben Lake, Wendy Craft, Jaycee Chapman, and Steven Wade. Clint Schipper held things together one six-month period when ADF terrorists plagued us the most. For many years Melanie Ebdon has supported my research with monthly donations to SCP; thank you, Melanie. Michael McCourt stepped in with financial support when I needed it most. Daniel and Nancy Farlow have helped out and were welcome visitors in 2018. The NSF funded the project early on. I am grateful to the Ugandan Government, the Uganda Wildlife Authority, the staff of the Toro-Semliki Wildlife Reserve, and the rangers and staff of UWA, too numerous to name, who made this research possible.

In addition to the research cited in Chapter 29, much of my perspective on bonobo society, social behavior, and distinctiveness was sharpened in

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In the very last stages of writing Bill McGrew helped enormously with Chapter 30. Thanks, Bill.

As I related above, my two doctoral co-supervisors were Loring Brace and Richard Wrangham, which means my academic pedigree is C.L. Brace–E.A. Hooton/W.W. Howells–A. Keith and R.W. Wrangham–R.A. Hinde–D. Lack/N. Tinbergen. I am proud.

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