Habitat Ecology and Primate Gregariousness in Nigeria's Gashaka Gumti National Park.

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I, Gonçalo Oliveira Paulino de Jesus, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

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ABSTRACT

Research presented in this thesis focusses on the interplay between plant and mammal communities within a unique West African biome: the mosaic savannah-forest habitat of the Gashaka-Kwano region in northeastern Nigeria. The major strands of investigation encompass habitat ecology and animal sociality as shaped by a significantly seasonal climate and revealed through analyses of a longitudinal data set.

The research is part of the *Gashaka Primate Project (www.ucl.ac.uk/gashaka),* one of West Africa's largest conservation and research initiatives, founded in the year 2000. The project operates in Gashaka Gumti National Park (GGNP) – a last remaining wilderness in the ecoregion that still harbours a biodiverse flora and fauna.

At GGNP, a pronounced fluctuation between an annual wet and dry season strongly influences the vegetation and corresponding wildlife as well as human subsistence. This marked climatic seasonality affects plant cover and fruit productivity, giving rise to a seasonal pattern of food availability that constrains wildlife ecology and shapes activity budgets and reproductive features. These dynamics are specifically explored with respect to an unhabituated community of chimpanzees, and two study troops of baboons – an entirely wild-feeding group, and another group that supplements its diet through crop-raiding. With respect to the latter, the thesis explores if and how constraints imposed by habitat seasonality can be buffered by the consumption of crops.

The current investigation capitalizes on the project's longitudinal repositories of base-line data covering a 13–year period (2002–2014), which were compiled, cleaned and analysed. The resulting thesis is broken down into seven chapters:

– Ch. 01 Research rationale. Importance of long-term data and focus on seasonality

– Ch. 02 The Gashaka Primate Project. Long-term research in Gashaka Gumti National Park

– Ch. 03 Seasonality in a savannah-forest mosaic. Climate and plant phenology

– Ch. 04 Chimpanzee gregariousness. Influence of abundance and dispersion of food patches

– Ch. 05 Baboon behaviour. Activity budgets and home range use

– Ch. 06 Baboon demography and reproduction. Comparing wild-feeding and crop-raiding troops

– Ch. 07 Outlook. Enabling research and conservation at a biodiversity hotspot

IMPACT STATEMENT

THE GASHAKA PRIMATE PROJECT: CONSERVING THE WORLD'S RAREST CHIMPANZEE

The research presented in this thesis was done through the *Gashaka Primate Project* (GPP), which is a biodiversity research project that uses field studies to stimulate efforts to conserve the world's most threatened chimpanzee in its natural environment. GPP focuses not only on chimpanzee studies, but also on long-term studies of other wild non-human primates (i.e. baboons and putty-nosed monkeys). A recurring theme of research is the recognition that considerable intra-specific variation is not only a hallmark of humans, but also of other animals. This contradicts traditional Cartesian views of animals as automatons that execute narrow genetic programmes or, as classic ethology posited, follow "instincts". Instead, primates in particular display behavioural flexibility to cope with ecological constraints. It is therefore of scientific interest to work towards the preservation of non-human primates in their natural habitats, as they serve as models that can help us understand the pathways and selective pressures that characterise human evolution and cultural diversity. Chimpanzees show the greatest degree of behavioural diversity amongst non-human animals and research led by GPP has corroborated the view that their communities are characterised by unique combinations of social customs and subsistence techniques.

GPP's work has established that this remote wilderness in the Cameroonian highlands holds the largest remaining population of the Nigeria-Cameroonian chimpanzee (*Pan troglodytes ellioti* aka *vellerosus*), perhaps 1,000 individuals. This ape is the genetically most distinct subspecies of chimpanzee, and by far the most endangered, with at most 3,500 individuals remaining - most of them in small pockets. All population fragments face severe anthropogenic pressures.

The bushmeat trade is thought to be the biggest threat to the survival of chimpanzees (as well as the other African apes). However, assessments of the reduction of wild populations are notoriously unreliable since they are mostly based on indirect evidence such as brief surveys of markets and interviews with hunters. GPP's team used a direct approach and measured annual loss from the wild through intake rates of chimpanzee orphans into sanctuaries in Africa. From this, the loss to wild populations was calculated by relating arrivals into sanctuaries to the proportions of infants in wild groups, hunting strategies, and the likelihood that captured babies make it to a sanctuary. The results suggested that current rates of hunting are many times higher than sustainable rates, and that the Nigeria-Cameroonian chimpanzee will go extinct in 20–30 years, if protection measures are not dramatically improved.

GPP also allows knowledge transfer between university and postgraduate students/ researchers from Africa and the developed world, who work alongside each other in the field. The scheme ensures that African students interested in research and conservation are exposed to state-of-the-art methods not otherwise available in Nigeria. The project also assists national park rangers in obtaining masters degrees and thus improving their career prospects.

Research done by GPP has contributed to wider cooperation towards conservation in West Africa. The project's research was crucial in the development of the *Regional Action Plan for the Conservation of the Nigeria-Cameroon Chimpanzee* (2011).

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Para a Avó Bia, o Avô Mário e a Vóvó Bia

In memory of Hammaunde, Bobbo and Buba

CHAPTER 01

RESEARCH RATIONALE

IMPORTANCE OF LONG-TERM DATA AND FOCUS ON SEASONALITY

General Theme: Dynamics of Plant and Mammal Communities

Research presented here focusses on the interplay between mammal and plant communities within a unique West African biome: the mosaic savannah-forest habitat of the Gashaka-Kwano region in northeastern Nigeria. The major strands of investigation encompass habitat ecology and animal sociality as shaped by a significantly seasonal climate.

The study area is located in Gashaka Gumti National Park (GGNP), one of the last remaining wildernesses in the ecoregion that still harbours a biodiverse flora and fauna. The study compiles and analyses longitudinal information assembled by the *Gashaka Primate Project* (*www.ucl.ac.uk/gashaka*), a research and conservation initiative operating in the park since the year 2000. In a pioneering effort, the thesis compiles and pools numerous hitherto untapped data sets, including as yet unreported background information on the occurrence and distribution of large mammals (chiefly, pigs, antelopes, primates) (*Ch. 02*). The longitudinal records are employed to reconstruct the habitat's climate, i.e., the sub- and supra-annual cycles of the area's weather conditions and its influence on changes in vegetation cover and fruit production of the dominating plants, i.e., densely growing forest trees and dispersedly growing savannah trees (*Ch. 03*). The research then focuses on the two major study species, chimpanzees (*Pan troglodytes ellioti*) and olive baboons (*Papio anubis*). A main aim of the chimpanzee investigation is to understand how annual fluctuations in fruit production impact on the pattern of fusion-fission sociality, as inferred from sightings of the apes and numbers of animals that built arboreal sleeping nests in close proximity (*Ch. 04*). The baboon research compares the influence of local ecologies on two study troops – one that feeds entirely on wild food sources, while the other supplements its diet through crop-raiding. The potential effects of crop-raiding *vs* wild-feeding are studied with respect to the general activity budgets and home range use (*Ch. 05*) as well as the demographic development of the troops and female reproductive parameters (*Ch. 06*). A final outlook (*Ch. 07*) provides examples of how the assembled long-term data sets can inform overarching research questions as well as a view of the dynamics increasingly faced by longitudinal field research: the destructive influence of human activities and corresponding efforts by researchers to design conservation measures.

A description of the study area, general methodology and some descriptive data on the large mammals inhabiting the study area (*Ch. 02*) serves as background for the following chapters of this study that present particular research findings (*Ch. 03* – *Ch. 06*) and which are preceded by an introduction into its specific topic as well as information about the particular methodology and methods. Using literature from the wider discipline, the following sections contextualize the rationale for the research by establishing the threads that will run through the thesis: its focus on environmental variation (both seasonal and supra-annual) which necessitate a long-term approach in terms of data collection.

The Perspective of Long-term Studies

The adaptive significance of behaviour, particularly social behaviour, and features of life history cannot be gleaned from investigations of captive animals (Kappeler *et al*. 2012). To understand the dynamics of selection processes, field studies are indispensable. However, research on wild-living primates is faced with several constraints (Robbins 2012) – such as that monkeys and apes are long-lived, that they tend to inhabit remote localities, and that they are typically hard to observe, because they avoid contact with humans. In addition, unlike investigations of, e.g., invertebrates, primatologists are hardly ever able to obtain large sample sizes. As a result, about a decade of research is needed to outline the basic ecological framework within which a species operates, about two to three decades are required to reconstruct developments of demography, and several more decades to understand how taxa respond to long-term changes in its habitat (ibid.; Hayes & Schradin 2017).

The current PhD thesis has to be read – and hopefully appreciated – against this general background. Its research is embedded in a long-term research effort structured by the *Gashaka Primate Project* (see *Ch. 02*). As is customary in longitudinal ventures, generations of volunteers, undergraduate and graduate students at the levels of master and doctoral thesis research as well as post-docs, established scientists and local field assistants have contributed to a pool of baseline data owned by the *Gashaka Primate Project*. These archives have been sighted, cleaned and organized as part of the present PhD thesis.

Typically, field-based student projects encompass between one and three stints in the field. As such, they can capture only a fraction of the environmental variation and the resulting responses of plants and animals to this fluctuation (Hayes & Schradin 2017). By collecting base-line data and feeding them into a common pool, these short-term studies can nevertheless lay the groundwork which – in a mode of positive feedback – enables better and better provisions of basic contextual information that benefit future short-term research (ibid.).

Consequently, records spanning numerous years on climate, habitat composition and productivity need to be combined with information on behavioural and demographic variation (Kappeler et al. 2012). In other words, to allow a better understanding of how environmental factors influence wildlife behaviour and gregariousness, a long-term perspective is needed with respect to two dimensions: (i) *ecology*, including sub- and supra annual variation of climate and plant production and (ii) *ethology*, including information on physiology, behaviour, grouping and life-history patterns.

In its broadest sense, *ecology* is the biological discipline that investigates the relations of organisms to their physical surroundings (abiotic factors) and to one another (biotic factors) – a concept made popular by the historic textbook *Fundamentals of Ecology* (Odum 1953). A *habitat* is the natural home or environment of an organism, as characterized by both physical features (elevation, soil, moisture, temperature range, light intensity, shelter opportunities) and biological features (disease vectors, food distribution, presence or absence of predators, partners for reproduction). Habitat types can be broken down by region (polar, temperate, subtropical, tropic) as well as mode (terrestrial, fresh water, marine water).

Records of day-to-day parameters of *weather* (e.g., mean and maximum temperature, humidity, rainfall) can be combined to construct an extended picture of the area's *climate*, i.e., the long-term weather conditions typical for an area – information that is crucial with respect to the longitudinal dimensions discussed above.

Habitats do not only experience inter-annual fluctuations, they are also subject to changes with vastly greater time depth. Very slow natural processes include tectonic uplift and subsidence, while other geomorphological events occur in more rapid temporal bouts (earthquakes, landslides, storms, flooding, wildfires, coastal erosion). Habitat change is also increasingly brought about by anthropogenic activities. Over the course of human evolution, humans altered habitats through fire regimes, farming practices and extraction of natural resources, with pollution, fragmentation, climate change and local or global extinctions of plant and animal species as a consequence. Nowadays, the extent of human interference seems to have become the dominant influence on global climate and environments.

Consequently, many scientists label the current geological age as the *Anthropocene* (Crutzen & Stoermer 2000, see also Hockings *et al*. 2015).

With respect to the dimension of *ethology*, Clutton-Brock & Sheldon (2010) identified various advantages of long-term, individual based wildlife studies: (i) analysis of age structure; (ii) linkage between life history stages; (iii) quantification of social structure; (iv) derivation of lifetime fitness measures; (v) replication of estimates of selection; (vi) linkage between generations.

The current research is able to capitalize on some, albeit not all dimensions of these long-term trajectories (see also Chapman *et al*. 2017), given its main focus on two taxa of primates – chimpanzees and baboons –, which form part of the attraction of why biologists work at Gashaka Gumti National Park. Apart from general census work, the main research – as already mentioned above – focuses on a specific community of chimpanzees in the vicinity of the Gashaka-Kwano research station (*Ch. 04*) and two study troops of baboons – one entirely wild-feeding group around the Kwano research station, and one group inhabiting the wider banks of the Gamgam river that supplements its diet by crop-raiding (*Ch. 05, Ch. 06*). The chimpanzees are not habituated to human observers that allow for individual recognition, but the members of the baboon troop are individually known and the demographic development of the troops monitored and recorded over generations – including a reconstruction of the particularly important (maternal) kin relations (Chapman *et al*. 2017). Thus, the current analyses can draw conclusions that necessitate individual recognition only with respect to the baboon study troops, but not the chimpanzees. Still, the chimpanzee data on grouping pattern (day parties, nesting parties) allow to contextualize them within the dimensions of long-term seasonality of climate and plant fruit productivity (for an appreciation of the interplay of changes in tree and primate communities, see Chapman *et al*. 2017).

Natural History vs. Hypothesis-driven Research

The research presented here includes both descriptive and quantitative elements, represented by the somewhat binary juxtaposition of inductive natural history vs. deductive hypothesis testing.

While the *natural history* approach does not have a strict definition, it can generally be understood as a non-experimental close-up inquiry of features of habitats and the organisms harboured in them – i.e., "descriptive ecology and ethology" (Greene 2005; see also Fleischner 2011). Another useful definition that sets it apart from "strict" science sees it as a practice that emphasises the observer's personal background. Indeed, many natural historians were and are unpaid non-professional enthusiasts, who like to spend time in the great outdoors to pursue their hobby, while also recording information. These aptly named "naturalists" enjoy the challenges of being immersed into a field-experience, which, for them, often incorporates an aesthetic component (Herman 2002). Great English naturalists of the 19th century such as Henry Walter Bates, Alfred Russel Wallace and Charles Darwin conducted natural history travels over many years, which ultimately helped to transform biology from a descriptive to an analytical science. Amateur collectors, natural history entrepreneurs and gentlemen scientists helped to build up some of the large collections of museums, that bear "natural history" in their names, such as the Natural History Museum, London.

This once so prominent Victorian style of conducting biological studies, while still embodied by natural history societies in the UK and elsewhere, is seemingly losing ground in comparison to more contemporary methodologies (Fleischner 2005). Still, as for Nigeria, the approach is institutionalized by the *Nigerian Field Society* (NFS). The organization was founded in 1930, when Nigeria was still a British colony. Nowadays a "national" organization, NFS maintains branches in cities such as Lagos, Kano and Abuja, but also a UK branch (*nigerianfield.org* [accessed 22Jul18]). In fact, some of the important botanical research of the wider Gashaka Gumti National Park area, as well as bird studies, were conducted by NFS members (e.g., Chapman & Chapman 2002, Wilkinson 2008).

The aesthetic and immersive elements of natural history-driven fieldwork certainly also contributed to my motivation to conduct research in West Africa. However, comparatively more time than outdoors was spent in front of computers, compiling and analysing data. This encompassed the curation of "natural history" accounts which may not immediately seem relevant to answer particular questions – such sightings of wildlife. These include species rarely directly encountered by observers, e.g., forest-dwelling leopards and shy blue duikers (cf. *Ch. 02*). Yet, their hidden presence in the study area may – as predators or prey respectively – impact considerably on the ways the study primates behave. The compilation of such descriptive natural history information can thus enable future syntheses (cf. *Ch. 07*).

For the most part, however, information provided in this thesis is not qualitative but quantitative and subject to the *hypothetico-deductive method* (cf. Godfrey-Smith 2003). Thus, the thesis formulates hypotheses and associated predictions that are subsequently tested against data (including descriptive elements). The statistical methods employed a mixture of exploratory data analyses (laying out main characteristics of the data set aided by summary tables and visual methods such as graphs) and confirmatory data analyses (testing statistical significance). Similarly, the investigation contains both confirmatory research (testing *a priori* hypotheses and outcome predictions made before the data were analysed) as well as exploratory research (generating *a posteriori* hypotheses while examining the data-set and looking for potential relations between variables).

In reality, however, data collected in the field over a long period of time will be confounded by many variables that can be difficult to tease apart or control for. Thus, as detailed inductive knowledge of natural history increases, observers will come across cases that are not encompassed by any single hypothesis or that they may contain elements of various hypotheses or require the formulation of altogether new predictions (see Quinn & Dunham 1983, for a discussion of the limits and unsuitability of a purely hypotheses-driven approach in ecological and evolutionary research).

Predominantly, field biologists are confronted by *stochastic* variables with a random probability distribution that cannot be predicted precisely – such as extreme climate abnormalities (storms, very dry or very wet years). Such sporadic and rare ecological crises are particularly likely to affect taxa such as primates, simply because they are long-lived (Chapman *et al*. 2017). These stochastic events may severely impact on life history variables, which raises the possibility that "fitness measures during average years might be less important than in years characterized by strong deviations in environmental conditions" (Hayes & Schradin 2017, p. 600). Consequently, extreme periods are probably more important in shaping the gene pool of a population than "normal" years (ibid.). Such realization is in conflict with the orthodox idea that fixed differences between individuals are prevalent and closely tied to differences in genotype and phenotype (see Clutton-Brock & Sheldon 2010, for an appreciation of this possibility).

For example, a predation event, an extensive drought or a hurricane may lead certain animals to perish and others to survive (male vs. female; young vs. old; dominant vs. subordinate), thus influencing social organization (Dittus 1985). A case in question concerns the emergence of a relatively peaceful and relaxed dominance hierarchy in a baboon troop once particularly aggressive males had died from tuberculosis, while atypically unaggressive males survived (Sapolsky & Share 2004). Conversely, a relatively cooperative mode of hunting that had developed in another baboon troop fell apart once personalities central to this tradition had perished (Strum 1987).

Again, we come full circle to appreciate that a comprehensive understanding of behaviour and social structure requires long-term data collection (Clutton-Brock 2012), but that even these repositories will not easily lend themselves to detect a reliable pattering of proximate causes (Cluttton-Brock & Sheldon 2010). The ultimate consequence is somewhat ironic, because "scientifically, long-term studies are not replicable" (Hayes & Schradin 2017, p. 601), neither within a given taxon nor among closely related species.

Therefore, while reporting observations made during long-term field research, biologists will need to accept the considerable limits of interpretation. This comprises the appreciation of the fact that numerous processes interact in ways which are impossible to disentangle in terms of direct causation – which renders it questionable to force observations into sets of artificially distinct hypotheses derived from debatable "null"-hypotheses (Quinn & Dunham 1983). Research unfolded in this thesis is subject to exactly this – hopefully fruitful – tension.

Climatic Seasonality and Phenology

As has been pointed out, the major strands of investigation of the current research encompass habitat ecology and animal sociality as shaped by a significantly seasonal climate.

In any given habitat, conditions are typically not constant throughout the year, i.e., more or less extreme changes may be observed, particularly in water availability, with knock-on effects for plant and animal communities. Some organisms are more tolerant of wide variations (*generalists*) while others are very specific in their requirements (*specialists*). The repeated patterning of these environmental conditions will lead to the formation of area-typical communities of plants and animals, i.e., particular *biotopes* or *ecosystems*. Thus, the recurrent fluctuations in rainfall, temperature, day-length and radiation constitute the *seasonality* of a particular biome (Brockman & van Schaik 2005).

The ecology sub-discipline of *phenology* (Osborne 2000) investigates periodically recurring developmental phenomena in the context of plant and animal life. For a habitat's flora, phenological markers may include the emergence of leaves and flowers and the production of fruits, i.e., the plant cover undergoes a succession of phenophases with often dramatic changes triggered by annual resp. supra- or sub-annual cycles in rainfall (Adamescu *et al*. 2018).

The seasonal climate with its corresponding cycles of plant productivity will affect the animals that rely on vegetal resources for diet or shelter (van Schaik *et al*. 1993). For example, depending on floristic developments, many animals display distinct peaks in reproduction and the raising of offspring. Moreover, as for primates, it has long been established that access to plant food, chiefly fruit, triggers related variation in social organization (Chapman *et al*. 2017).

Gashaka Gumti National Park is no exception to these cascading effects brought about by climatic fluctuations. In fact, a central topic of the current research relates to its severe seasonality in rainfall. In fact, the study area experiences a rather extreme annual fluctuation between a dry and a wet season – with about 5 months (from roughly November to March) not experiencing any (or very little) rainfall, followed by a built-up to a rainy season with most precipitation during September (*Ch. 03*). The effects of this severe seasonal pattern will be tracked via long-term data for the phenology of plants (Ch. 03) and associated responses of wildlife, in particular the grouping pattern of chimpanzees (*Ch. 04*) as well as baboon behaviour (*Ch. 05*) and reproduction (*Ch. 06*).

Animal Responses to Seasonality

The current research investigates the influence of habitat seasonality chiefly for diverse groups of primarily large mammals (note: for Latin names of animals mentioned in this introduction, see *Ch. 02*). These include aardvarks, carnivores, hares, hyraxes, rodents, scaly ant-eaters, ungulates and, as already mentioned, primates (Kingdon *et al*. 2013; for overviews to primate taxonomy, biology, ecology, sexuality, sociality and cognition that track the discipline's development, see classic collections and textbooks: Smuts *et al*. 1987, Dunbar

1988, Martin 1990, Strier 2011, Campbell *et al.* 2012, Mitani *et al.* 2012, Dixson 2013, Rowe 2016). The current study excludes data on birds, although the research area is a mecca for bird watchers (GGNP is an IBA, i.e., important bird and biodiversity area; *www.birdlife.org*). Interesting anecdotal data will refer to some rare carnivores (*Carnivora*) like the leopard (*Panthera pardus*) and the African golden cat (*Felis aurata*), while quantitative data are restricted to ungulates and primates.

Apart from primates (see below), ungulates are the most prominent group of large mammals spotted and identified with regularity, both during foot surveys as well as on footage of stationary traps (still-camera, video-camera). As their name indicates (Latin *ungula*, "hoof"), these primarily large mammals use the tips of their toes to sustain their body weight while moving. They include the odd-toed ungulates (*Perissodactyla*) such as horses and rhinoceroses, and the even-toed ungulates (*Cetartiodactyla*) such as pigs, giraffes, camels, deer, hippopotamuses and bovids. While some members are omnivorous (pigs), many ungulates are herbivorous – and, as is the case in ruminants , gut bacteria allow them to digest cellulose. The study at Gashaka-Kwano yielded quantifiable data largely for two types of pigs – red river hog (*Potamochoerus porcus*), giant forest hog (*Hylochoerus meinertzhageni*) and three types of bovid (*Bovidae*) resp. antelope – buffalo (*Syncerus caffer*), bushbuck (*Tragelaphus sciptus*) , yellow-backed duiker (*Cephalophus silvicultor*).

For the study area's primates, direct observations are easily possible for the various monkey species – black-and-white colobus (*Colobus guereza*), tantalus monkey (*Chlorocebus tantalus*), mona monkey (*Cercopithecus mona*), putty-nosed monkey (*Cercopithecus nictitans*), with olive baboons being the subject of detailed study. As mentioned above, chimpanzees are the other focal primate; these apes are not that easily seen by researchers, i.e., they are not habituated to human presence. However, chimpanzees leave indirect signatures of their past behaviour, such as sleeping platforms (nests) and abandoned stick tools with which they harvested honey and ants, and they can often be heard vocalising.

The current research will often refer to particular modes in which animals engage with each other. For this, it should be kept in mind that there is no commonly accepted terminology to denote the ways animals distribute themselves spatially and / or interact with members of their own species. Helpful might be a distinction between the following two terms. *Gregariousness* can be perceived as a broad umbrella term, which accommodates occasional solitariness as well as permanent grouping without implying specific modes of interaction. It can be used to describe herds of individual ungulates that forage together in a savannah or aggregate at a waterhole as well primates that spread out in a fission-fusion way (see below) across the landscape, but maintain individualised relationships (Wolff 2003) The term *sociality* leans more to the actual modes of how animals associate in *social groups*, several of which make up *societies* (MacKinnon & Fuentes 2011)

Throughout the thesis, it will be explored if and how habitat seasonality influences the behaviour and reproduction of the study animals. Detailed predictions, preferentially related to competing hypotheses, are developed during the specific data chapters – while a few examples of investigatory routes are sketched out in the following.

Chimpanzee communities split into sub-units, so-called "parties". Correspondingly, the study will investigate if and how the seasonally varying abundance of fruit and its spatial distribution affects the sizes of (foraging) day parties resp. (nesting) night parties, the number of animals that build sleeping platforms in close proximity (cf. Newton-Fisher *et al*. 2000, for a review of factors that may influence party size).

For the study baboons, the thesis will investigate if and how seasonality affects the partitioning of basic activities (travel, forage, rest) throughout the year. For example, it might be expected that in times of plenty, animals may use their mental map to move more goal-directed from one rich food patch to the next, ignoring opportunities along the way to forage in less promising locales – something they may do when food sources occur more scarcely (Johnson *et al*. 2015). As a result, their travel speed and thus the overall time spent travelling should decrease. Alternatively, as rich sources such as fruit tend to grow in small patches that are quickly depleted, longer day ranges may be expected.

The fact that one of the study troops is entirely wild feeding, while the other supplements its diet through crop-raiding will allow for an interesting comparison (cf. Paterson & Wallis 2005). For example, it may be expected that crop-raiding animals will need to invest less time in travel (given that cultivated fields yield more sources than patches of wild food) and in foraging (given that crops will need less time to process and are of higher caloric value). As a further consequence, it may be expected that crop-raiding baboons have shorter birth intervals. Crop-raiding may also allow the baboons to reproduce non-seasonally, because there will be fewer bottle necks for the optimal times to conceive, be pregnant or wean infants (Emery Thompson 2016).

While previous researchers have already looked at the differences between the study troops in terms of habitat, reproduction, diet, stress and activity patterns (cf. Warren 2003, Higham 2006, Lodge 2012; details in *Ch. 05*, *Ch. 06*), this thesis expands these findings, using much larger data sets. The various predictions will be evaluated against the available data.

The Challenge of Conservation

The last fifty years have seen a proliferation of primate-focused field research, whether in South America, Africa – including Madagascar –, or Asia, and dozens of these projects are meanwhile going on since more than a decade. While originally motivated by purely "scientific" interest, these projects have, since about the early 1980s, often mutated into ventures that are also concerned with nature conservation (Kappeler et al. 2012). Long-term projects are particularly suited for such commitment, because the scientific questions they aim to answer cannot be pursued if the study animals and the habitats they depend on are wiped out. Conversely, long-term studies can generate information about the changing status of populations as related to human disruption, and as such provide a foundation for the development of conservation strategies (Hayes & Schradin 2017). Thus, longitudinal research has become an increasingly important catalyst for protective activities at the local or regional scale (Clutton-Brock 2012).

Field work at Gashaka Gumti National Park is embedded in exactly this trajectory. As with many other study habitats, the reserve's fauna and flora is threatened by anthropogenic disturbances such as hunting, land conversion and extractive industries. Consequently, I have not only spent time and energy as a researcher, but have worked with the *Gashaka Primate Project* to initiate numerous capacity building projects for the benefit of local communities and the national parks service, as well as outreach activities that include public engagement events and the development of exhibitions by contemporary artists who had spent residencies at the field site (see *Ch. 07*).

Thus, apart from its efforts to render long-term data fruitful for an analysis of how a West African seasonal environment impacts on plant communities and with this on the sociality of primates, this research also reflects the challenges and opportunities for field studies to become active in nature conservation (Tranquilli *et al*. 2014).

CHAPTER 02

THE GASHAKA PRIMATE PROJECT.

LONG-TERM RESEARCH IN GASHAKA GUMTI NATIONAL PARK

Fig. 02.01. Panoramic view across the central part of the Gashaka section of Nigeria's Gashaka Gumti National Park. Ridges of the Mambilla plateau are visible on the horizon (02Sep09). (Photo: GJ)

Merits and Constraints of Long-term Studies

Wildlife ecologists and behaviourists alike have since long recognised the importance of running longitudinal studies (e.g., Clutton-Brock & Sheldon 2010, Kappeler *et al.* 2012, Robbins 2010), because they can offer detailed insights into evolutionary pressures. In particular, investigations based on individually identified animals that are, ideally, followed from birth till death, allow to address crucial questions related to ontogeny, behaviour, and life-history. At the same time, such long-term efforts face considerable challenges and constraints related to the logistics of running such research over a lengthy period in what are often remote locations (ibid.).

The current PhD thesis has grown out of the long-term research and conservation efforts of the *Gashaka Primate Project* (*www.ucl.ac.uk/gashaka*; Sommer & Ross 2011a), operational since the year 2000 in the Gashaka Gumti National Park in Northeastern Nigeria. The analyses of long-term data presented in this thesis will inform and enable future work at the site and future analysis of still untapped data sets. It is therefore critical to lay out the complex processes and limitations of collecting and analyzing various data sets. The following overview into the current study's background therefore aims to detail the physical infrastructure of the project, how study site and study animals are embedded into the wider ecological context, the regime of data collection, data curation and data analyses, with focus on my contribution.

The current study derives its origin and justification from a common problem associated with long-term studies, i.e., the fact that information about habitat ecology as well as animal behaviour and demography accumulate as a function of the growing number of researchers, students and field assistants contributing to the collection of base-line data. This requires strategies and policies for data management and storage, as well as resources to curate these sets of information (Kappeler *et al.* 2012). However, such a perspective extends past the typical duration and aims of the rather short-term research objectives associated with, e.g., a master or PhD thesis or individual research project (Hayes & Schradin 2017). Moreover, to achieve acceptable standards of inter-observer reliability and thus maintaining consistency and quality of data collection is not an easy task (Clutton-Brock & Sheldon 2012, Kappeler *et al.* 2012).

The current thesis has to grapple with exactly this tension of opportunity and constraint. On the one hand, the thesis utilizes the opportunity to exploit data that have been amassed over one and a half decade, i.e., over a period a single researcher can hardly ever cover on his or her own. On the other hand, the longitudinal nature of the study reflects a significant investment and energy to critically compile, scrutinize and clean numerous sets of data that were collected by generations of students, volunteers, researchers and field assistants. This entailed to deal with such idiosyncrasies as different types of handwriting in paper-based protocols or the fact that some data sheets were lost or destroyed by insects or rodents.

Still, these are the realities of field-based long-term research, and while the resulting data may not be perfect, they are the best window into the ecology, behaviour, sociality and reproduction of plants and associated wildlife, in particular monkeys and apes, in what is an increasingly fragile ecosystem in Western Africa (Oates *et al*. 2004).

The results of the current research are based on assorted long-term data sets collected by affiliates of the *Gashaka Primate Project*, consolidated and analysed by me, the author of this thesis (GJ). To enable this, I spent time in Nigeria from 05Jan09–11Mar09, 03Aug09–03Oct09, 03Mar10–05May10, 11Apr11–13Jun11, 24Mar12–30May12, 22Mar13–22Apr13, amounting to a total of 11 months. During these periods, I was involved in diverse aspects of field work, from floral phenology to wildlife surveys to socioecological investigations of baboons and chimpanzees. The tasks covered, to various degrees, supervision and training of field assistants, volunteers and student researchers, designing field protocols, actual data collection, as well as curating existing and newly accumulated information (paper protocols, videos, photos, GPS files, weather records) and biological samples (herbarium, faecal samples, skulls).

The time subsequently required to analyse data far exceeded periods spent in the field. However, field work allowed a clear understanding, from first-hand experience, of the constraints and limitations of information contained in protocols written up by different individuals. In addition, the field work provided a genuine familiarity about the climate pattern, the plant cover, the species of wildlife and the behaviour of apes and monkeys, even if analysed data were collected outside my own residency at the site.

The periods and parameters of data collection are summarized in *Tab. 02.01* – including my particular contributions. Methodological specifics of data collection and a critical assessment of their potential constraints are introduced and discussed before results about the five general categories are presented:

– Ch. 02: Large mammal surveys (pp. 25–60);

– Ch. 03: Climate and plant phenology (pp. 61–113);

– Ch. 04: Chimpanzee grouping pattern (pp. 114–145);

– Ch. 05: Baboon activity pattern (pp. 146–185);

– Ch. 06: Baboon reproduction (pp. 186–230).

To prepare the reader for the result-based chapters, the following sections outline general features of the study area's (a) localities and logistics, (b) habitat seasonality and plant cover, and (c) assemblages of wildlife (large mammals). The outline incorporates and updates earlier descriptions developed earlier in conjunction with co-researchers (Sommer & Ross 2011, Pascual-Garrido 2011).

Tab. 02.01. Long-term data sets utilised, i.e., designed, collected, curated, compiled and/or analysed by GJ. Site K (Kwano) = forest-savannah habitat inside National Park, habitat of chimpanzee and wild-feeding baboon study group. Site G (Gamgam) = forest-savannah habitat and cultivated field at park's edge near human settlements, habitat of crop-raiding baboon study group.

						Author's contribution: Y = yes, N = no, P = partial				
Thesis chapter	Focus	Type of data collection	Site (K = Kwano, G = Gamgam)	Parameters	Period covered	Design of regime of data collection	Actual data collection	Data transcription, computer input	Data transformation	Data analysis
Ch. 02	Study site wildlife (large mammals)	Foot surveys	K	Animal type, group size, group compostion, location	2005–08	N	N	Y	Y	P
		Video camera traps	K	Video clips	2012–14	P	N	Y	Y	Y
		Still camera traps	K	Still photos	2012–13	Y	Y	Y	Y	Y
Ch. 03	Habitat phenology	Climate, weather	K, G	Rain, temperature (min, max), humidity	2000–12	N	P	P	P	Y
		Botanical records of transect trees	K	Flowers (presence, colour), fruits (presence, number, colour, ripeness), feeding remains (presence, animal)	2002–12	N	N	P	P	P
Ch. 04	Chimpanzees	Habitat survey	K	Time, location; day group size and composition; vocalisations, drummings	2001–02, 2005–08	N	N	Y	Y	Y
		Chimpanzee nesting tree survey	K	Location; night group sizes	2012–13	Y	N	N	Y	Y
Ch. 05	Baboons (ecology)	Activity profiles	K, G	Time, habitat-type, activity, subgrouping	2004–11	N	N	Y	Y	Y
		Home range utilisation	K, G	Time, location (GPS coordinates)	2012–13	Y	N	Y	Y	Y
Ch. 06	Baboons (reproduction)	Demography	K, G	Individuals present, births, deaths, emigration, immigration; group sizes	2002–14	N	P	Y	Y	Y
		Reproduction		Female reproductive states (menstruation, cycle length, pregnancy, inter-birth intervals)	2002–14	N	N	Y	Y	Y

Kwano and Gamgam Study Sites in Gashaka Gumti National Park, Nigeria

Data presented here rely on field work carried out by the *Gashaka Primate Project* (GPP) in Nigeria's Gashaka Gumti National Park (GGNP) (*Fig. 02.02*). The reserve lies in southern Taraba State in eastern Nigeria, directly bordering Cameroon (06° 55' – 08° 13' N and 11° 13' N – 12° 11' E). Created in 1991, the park covers 6,731 km^2, which makes it the largest of Nigeria's 7 national parks (see Dunn 1999, Adanu *et al*. 2011).

The park's northern sector is named after the village of Gumti and stretches far into neighbouring Adamawa state. The Gumti sector is a flat biome of grassland with small trees, and was until recently home to iconic savannah fauna such as elephant (*Loxodonta africana*), spotted hyena (*Crocuta crocuta*), wild dog (*Lycaon pictus*), lion (*Panthera leo*), roan antelope (*Hippotragus equinus*) and giant eland (*Taurotragus derbianus*). The southern Gashaka sector is named after the small village of Gashaka, once politically important during the 19th century Islamization of this part of sub-Saharan Africa. The mountainous Gashaka sector includes lowland (< 825 m), sub-montane and montane (> 1650 m) strata, rising to 2,419 m at Gangirwal, the "Mountain of Death", Nigeria’s highest peak on the Chappal Waddi escarpment (Gumnior & Sommer 2012).

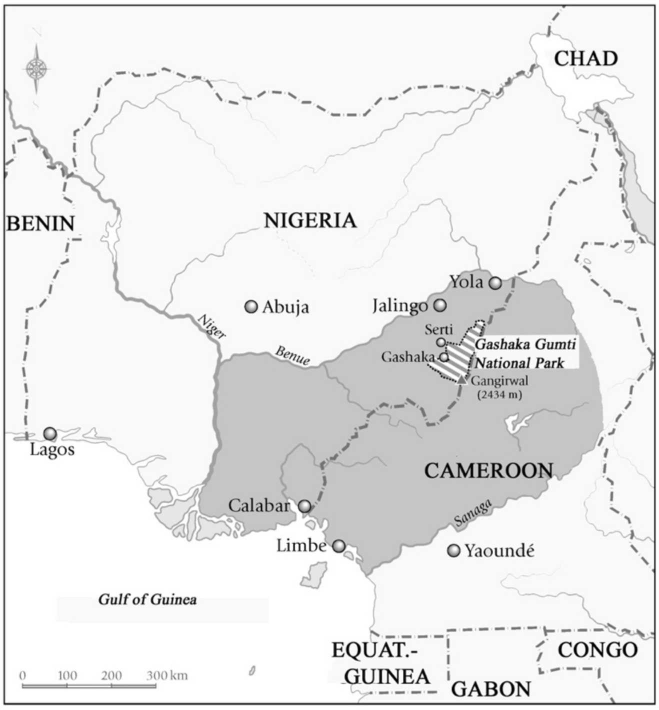


Fig. 02.02. Location of Gashaka Gumti National Park within the approximate historical distribution of the Nigeria-Cameroon chimpanzee *(P. troglodytes ellioti aka vellerosus)*, shown as hatched area. (Map: GPP / Maren Gumnior; from Sommer & Ross 2011b: Fig.1.2)

The biotopes of the wider Gashaka area face numerous imminent threats to their conservation (Adanu *et al.* 2011, Nyanganji *et al.* 2011; see Ch. 07). These include cattle grazing and burning of grass at the advent of the dry season to extend pasture grounds and stimulate sprouting of new vegetation, resulting in erosion of top-soil. Hunting for bush-meat is common, with poaching spilling over into the park itself. The core study area itself, however, has remained relatively safe from destruction, i.e., the field sites of Gamgam and Kwano near the village of Gashaka (see below).

The logistics of field work at GGNP are demanding. The *Gashaka Primate Project* maintains two research stations (*Fig. 02.03*). A 5-room house is sited near the village of Gashaka, at the edge of GGNP (elevation 320 m; 07° 21' N – 11° 29' E). About 11 aerial km from Gashaka and inside the park boundaries is the much larger 16-room station of Kwano, constructed at the site of a small village that was abandoned when GGNP was created (elevation 583 m; 07° 19' N – 11° 35' E). There is no mobile phone coverage at the field sites and connecting to the internet will often require travel of hundreds of kilometres.

A dirt road of 35 km, suitable for 4-wheel drive vehicles, connects Gashaka with the town of Serti and the national park headquarters at nearby Bodel. An ancient footpath links Gashaka with Kwano, and leads up into the highlands. This path, improved by Germany colonial forces in the late 19th century during their occupations in West Africa, is the main connection to enclaves on the escarpment and on to Cameroon (traffic approx. 1 person / h). The Gashaka-Kwano leg, at the onset of the dry season, is at time widened so as to allow access of 4-wheel drive vehicles. However, for more than half of the year can the Kwano site only be accessed on foot or by motorcycle, and the trek requires challenging river crossings during the rainy season.

Permanent power-supply is available at Kwano since early 2005 when a team of German engineering students erected a small plant, the so-called "power-island" – a hybrid facility with solar panels supplemented by hydroelectric power from a small nearby waterfall. At the same time, the *Gashaka Primate Project* also erected a repeater station on a steep hilltop, allowing for radio-communication with walky-talkies throughout much of the park.

Fig. 02.03. Research stations. (a) Kwano station: Sleeping quarters, office buildings and "power-island" (hybrid facility for harnessing of photovoltaic and hydro-electric power. 06Feb11). (Photo: Volker Sommer) (b) GPP sign at the Gashaka station in the village of Gashaka.

The thesis investigates the phenology of plants and animals at the wider Kwano site and basic socioecological features of three primate study groups – a crop-raiding baboon study group at Gamgam and another, wild-feeding, baboon study group at Kwano, plus a chimpanzee community that inhabits the Kwano area (*Fig. 02.04*, *Fig. 02.05*).

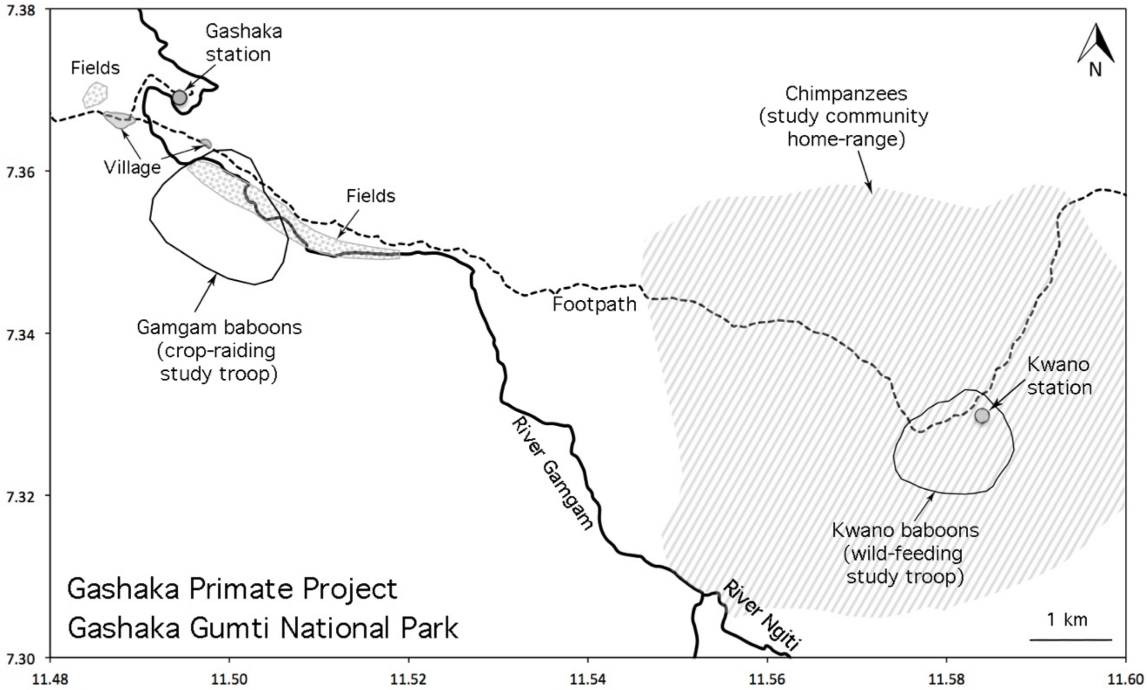


Fig. 02.04. Major study area. The map indicates locations of the two research stations (circles) at Gashaka and Kwano, as well as home ranges of the two baboon study troops (solid lines), i.e., the crop-raiding Gamgam troop near the village of Gashaka, and the wild-feeding Kwano troop further inside the national park. The home range of the chimpanzee community in the vicinity of Kwano (hatched area) is largely sympatric with the area from where most data on wildlife were collected. (Map: GJ)

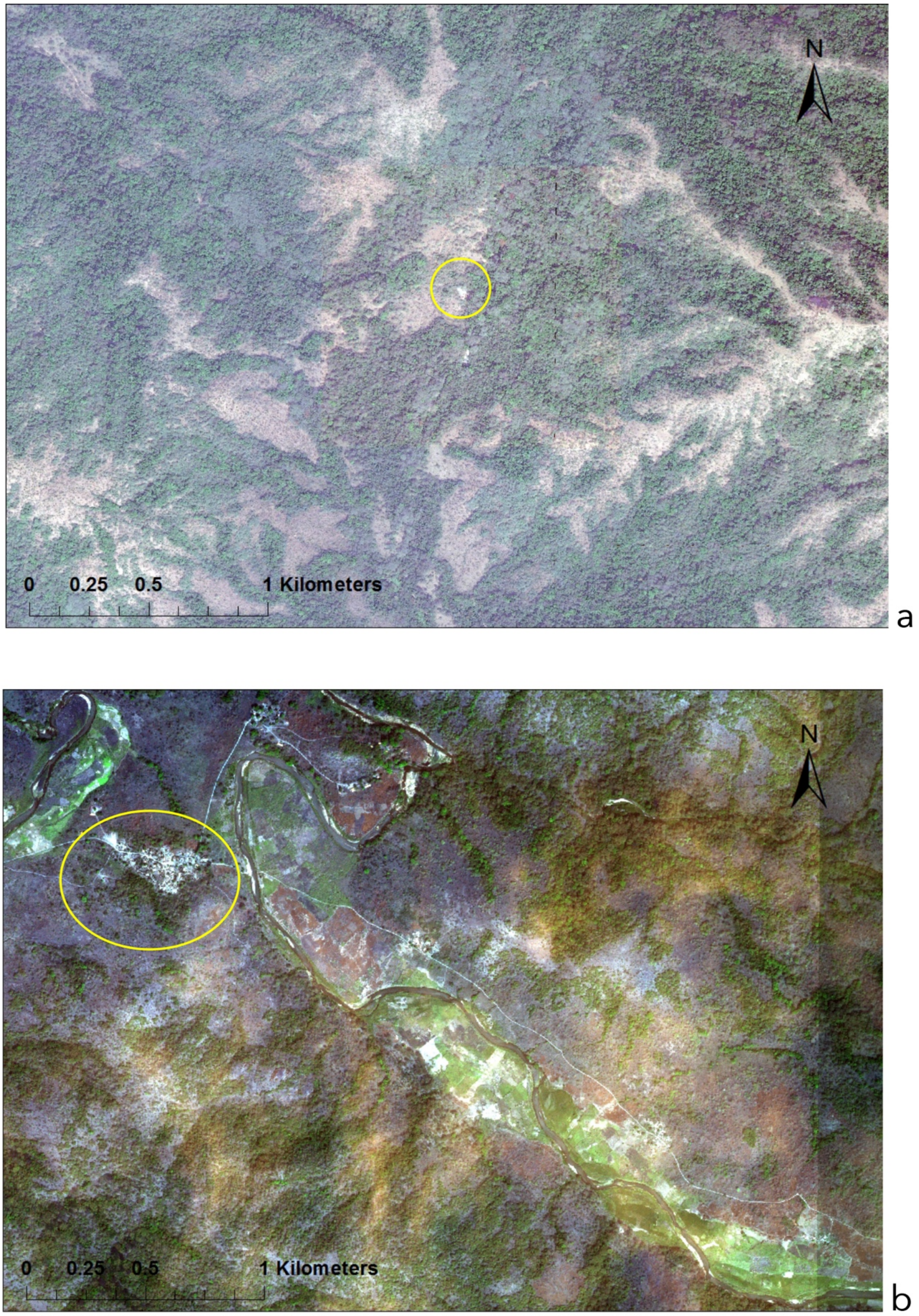


Fig. 02.05. Remote sensing scenes. (a) Savannah-forest mosaic around the field station of Kwano (circled). (b) Mosaic of savannah-forest and adjoining fields along the river Gamgam near the village of Gashaka (circled). (Remote sensing images: GPP / Maren Gumnior, Universities of Frankfurt and Gombe; edited by GJ)

The Kwano site is difficult to navigate for researchers, apart from the footpath connecting Gashaka with the highlands, given its often-steep terrain and dense plant cover. Therefore, trails have been cut with machetes to facilitate movements – a total of 79 km, marked every 25 m with permanent and successively numbered metal tags, which also label the footpath. In addition, a botanical phenology transect cuts through the Kwano site, which has 2 parts of 4 km each (*Fig. 02.06*).

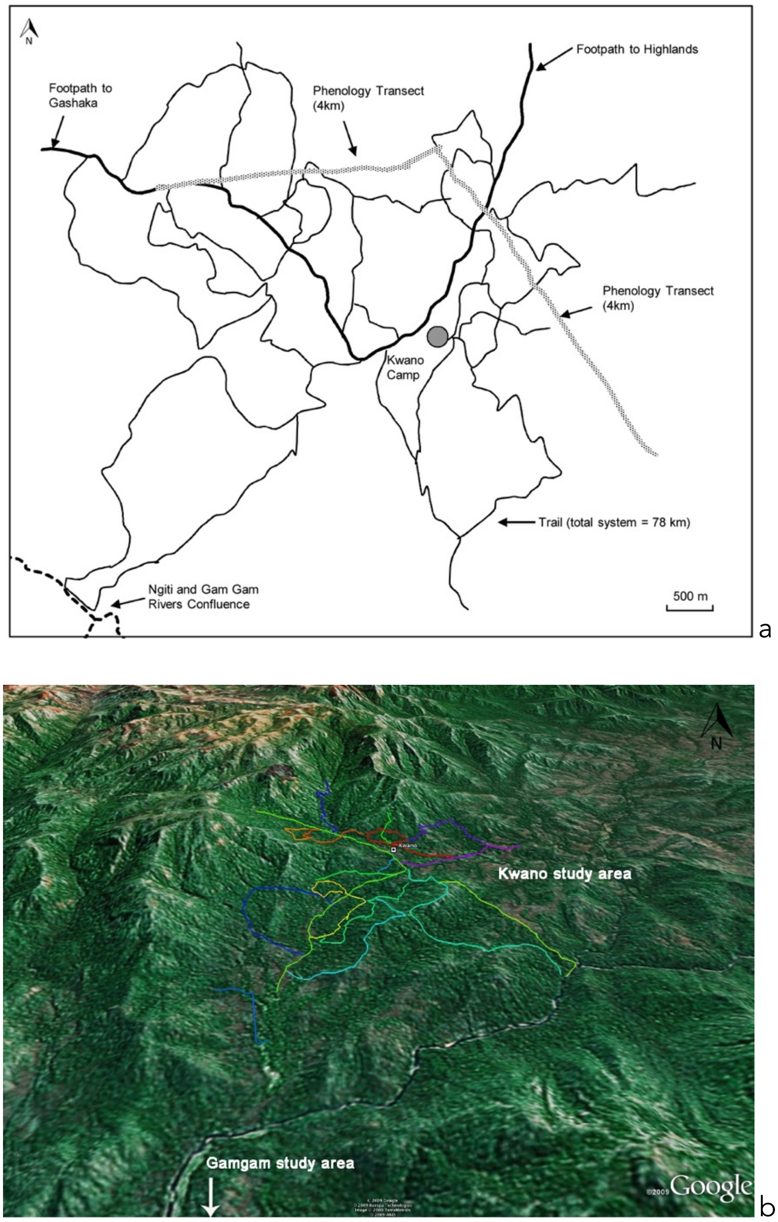


Fig. 02.06. Research trails and transects at Kwano field site. (a) Map of the Kwano study area showing the network of trails used by researchers and field assistants. A grey line indicates the 4 km long, phenology transect, with 1000 marked trees and adjacent vines. (Map: GJ) (b). System of research trails (78.7 km; different colours indicate different trails) in the Kwano study area. Three-dimensional representation of trail system based on images from "Google-earth". The Gamgam study site is located outside the image in continuation of the river valley. (Design: GJ)

The administrative centre of GPP is the Department of Anthropology at University College London (UCL), home institution of GPP's founder and director, Volker Sommer. Studies that focus on baboons are coordinated and overseen by Caroline Ross, Centre for Research in Evolutionary Anthropology at Roehampton University in London. (The following is an update of Sommer & Ross 2011a).

An ever-growing network of collaborators with the *Gashaka Primate Project* spans 35 institutions in 11 countries. With respect to capacity building, it is important that 9 partner institutions are based in Nigeria itself. Involved are also a further 7 from Germany, 6 from the USA, 5 from the UK, while the Czech Republic, Ivory Coast, Denmark, Portugal, Spain, Switzerland and New Zealand are also represented. Individual collaborators were affiliated with 25 universities (Federal University of Technology at Yola (Modibbo Adama University of Technology), Taraba State University Jalingo, Gombe State University, Federal University of Technology Bauchi, University of Maiduguri, American University Yola, Ibadan University, University of Cocody-Abidjan, Humboldt-Universität Berlin, Oxford Brookes University, Albert-Ludwigs-Universität Freiburg, Universität Frankfurt, Universität Würzburg, University of Neuchâtel / Switzerland, University of Copenhagen, Universidad Complutense de Madrid, Universidade Tecnica de Lisboa, University College London, Roehampton University London, University of St. Andrews, California State University Fullerton, University of Alabama at Birmingham, University of California Berkeley, University of Chicago, University of California Riverside, University of Canterbury New Zealand), 5 research institutes (Academy of Sciences of the Czech Republic Bron; Deutsches Primatenzentrum, Göttingen; International Institute for Tropical Agriculture, Ibadan; Leibniz-Institut für Zoo- und Wildtierforschung, Berlin; Max-Planck-Institut für Evolutionäre Anthropologie, Leipzig), 2 zoological societies (Zoological Society of San Diego; North of England Zoological Society), 2 conservation NGOs (Nigerian Conservation Foundation, WWF-UK) plus the Nigeria National Park Service.

Over the years, students (at the level of undergraduate, master, PhD), researchers (post-docs and senior), artists and journalists as well as volunteers have come from 22 countries of all 5 continents to collect data or to assist with capacity building within the GPP framework (Argentina, Austria, Cameroon, Canada, France, Germany, Greece, Italy, Ivory Coast, Japan, Mexico, New Zealand, Nigeria, Portugal, Spain, Sweden, Switzerland, Taiwan, The Netherlands, United Kingdom, USA).

The project employed up to a dozen field assistants that accompany researchers into the field or are engaged in the collection of routine data sets. All team members, apart from their specific objectives, contribute to the physical maintenance of the research stations and assist in the collection and compilation of long-term data (e.g., climate and phenology; demography and basic activity pattern of two habituated baboon study groups; chimpanzee vocalisations and nesting habits; encounters with other wildlife; camera-traps). In exchange, individual researchers may use certain parts of the long-term data set for own purposes. The resulting research papers are typically multi-authored, with the person who analysed the data set becoming lead author.

Over 20 years of activity (1999–2018), project output includes 217 publications (*APPENDIX 1*). A fair proportion is "grey literature", in form of 22 reports to donors and supporters. Moreover, research at undergraduate and graduate level yielded 62 degree-related write-ups – including 4 bachelor and 39 master's dissertations. A total of 19 PhD theses are based on GPP project work, with 15 already completed. Dozens of abstracts of talks and posters – a total of 45 – testify to the participation of GPP affiliates at conferences. The hard currency of science is, of course, research articles. GPP affiliates so far produced 65 in peer-reviewed journals and edited volumes.

Research within the framework of the *Gashaka Primate Project* is – increasingly so – not restricted to "classic" ecological and behavioural field studies of non-human primates, but includes topics from a variety of disciplines such as: taxonomy (in particular collembola, flies, ants, frogs, amphibians, birds), anatomy, genetics, biogeography, parasitology, endocrinology, nutrition, reproductive physiology, gestural and vocal communication, cognition, developmental psychology, ethno-botany, botany, meteorology, geography, human-wildlife conflict, ethno-primatology ("folklore studies"), social anthropology, public policy, contemporary arts and philosophy. This is, of course, a reflection of a developing tendency to combine field work with laboratory research and to aim for inter-disciplinarity. The current thesis reflects this trend which has spawned the idea to ultimately transition the *Gashaka Primate Project* into a *Gashaka Biodiversity Project.*

Habitat Seasonality and Plant Cover

A pronounced fluctuation between wet and dry season strongly influences the vegetation and corresponding wildlife as well as human existence in the Gashaka region (details on climate and associated changes in *Ch. 03*). Thus, for about 5 months, from mid-Nov till mid-Apr, very little rain falls, and mostly none at all. A dry dusty wind, the *harmattan*, may blow from the Sahara. The skies clear again once heavy downpours get going from about mid-Apr. The distinct climatic seasonality is reflected in the vegetation cover (*Fig. 02.07*, *Fig. 02.08*).

Fig. 02.07. Distinct seasonality shapes plant phenology in Nigeria's Gashaka Gumti National Park – and with it wildlife activity. (a) Forest plot at the height of the wet season (Jun-Oct). (b) The same plot during the dry season (Dec-Mar). Note cut tree in lower right corner). (Photos: courtesy of 2010 GPP vegetation cover survey, directed by Maren Gumnior)

a

b

Fig. 02.08. Gashaka area habitats. (a) Woodland-savannah at the onset of the rainy season when burnt grass begins to sprout. (b) Lowland rainforest. (c) View of the Gamgam study area across the Gamgam River valley towards forests around Kwano, shrouded in mist, during the wet season. (d) View of the same area, during the dry season. (Photos:)

Terrain in the southern Gashaka sector of Gashaka Gumti National Park is rugged, with altitudes from about 300–2,400 m, which include the northern outcrops of the Cameroonian Highland chain. Habitat types represent the diversity of Taraba as a whole, including Guinea savannah-woodland, riverine and gallery forest, lowland rain forest, montane forest and montane grassland (Akinsoji 1996). Forests around the extensive Gangirwal escarpment serve as a sponge-like repository for wet-season precipitation, releasing water slowly but steadily, so that abundant rivers flow continuously within the park's boundaries, even during the height of the dry season. GGNP is thus the major source for Nigeria's second-most important watercourse, the Benue.

A belt of savannah landscapes, about 1,500 km broad, in parallel alignment with the equator further south, characterises much of West Africa. Only 100–600 mm rain fall in the most northern savannah belt, the Sahel Zone, whereas the adjoining Sudan Zone sees up to 1,000 mm rain, with correspondingly higher tree densities. The Guinea zone, with up to 1,500 mm rain, borders against what was once contiguous rainforest (Reikat 2002). Though the Gashaka area is thought to be part of the Guinea Zone, its average rainfall is considerably higher – perhaps because of the nearby moisture-trapping peaks of the Cameroonian highlands.

With rain exceeding 2000 mm (see *Ch. 03*), one would expect a rather extensive forest cover. However, while forest, more or less closed, is indeed prominent (see *Ch. 03*), the landscape is blanketed in a mosaic of forest and savannah-woodland. This pattern could result, at least partly, from iron concretions in the soil. However, there is strong evidence that much of the savannah is derived, as a result of anthropogenic influences dating back centuries, if not millennia. The yearly burning of grass, done deliberately for about 3 months from Dec onwards, keeps large areas as grassy woodland – and prevents what would be a natural succession towards semi-deciduous forest (Louppe *et al.* 1995). The ancient habitat thus probably resembled a mosaic of moister and drier, semi-deciduous forests, which were then gradually replaced by woodlands with trees that are fire-resistant (pyrophitic). A human-made origin must also be assumed for the grassland of the higher elevations.

Still, there is no doubt that the dynamics of the region are largely climate-driven and that a pronounced seasonality aided the past development of a complex assemblage of vegetation cover.

Surveys of Non-Primate and Primate Mammals

Wildlife at Gashaka Gumti National Park

GGNP borders the north-eastern edge of West Africa's moist Guinean forest ecoregion, a biodiversity hotspot (Oates *et al.* 2004) that harbours almost a quarter of mammalian species endemic to continental Africa (Kingdon *et al*. 2013, Darwall *et al.* 2015). Within the boundaries of the large park, mammalian wildlife is likewise very diverse (Dunn 1999).

The following chapter is restricted the mountainous Gashaka sector and the specifically the study sites of Kwano and Gamgam. The focus is on "large mammals", i.e. those that, as adults, weigh more than 200 g. (The smallest large mammal would thus be the galago, see below.) The principal taxa are ungulates (antelopes, pigs) and primates (monkeys, apes). Still, GGNP is also home to a vast array of important non-mammalian vertebrates – including large species such as the Nile crocodile (*Crocodylus niloticus*) and the Rock python (*Python sebae*) –, such as rare fresh-water fish that thrive in the translucent rivers, and, with more than 500 feathered species, the place is an IBA (important bird area; see, e.g., Wilkinson 2008; see Dunn 1999 for a substantial compilation of bird taxa occurring at GGNP).

The quantitative part of this research is restricted to about a dozen or so species observed with regularity. However, the surveys also yielded important anecdotal – i.e. qualitative – information about elusive large mammals at Gashaka Gumti National Park that before have reportedly never or rarely been seen by the "naked eye" – such as golden cat (*Felis aurata*), leopard (*Panthera pardus*), honey badger (*Mellivora capensis*), or spot-necked otter (*Lutra maculicollis*).

The emphasis on large mammals is largely pragmatic, given the primate-focussed nature of the *Gashaka Primate Project*, and a concurrent lack of expertise with respect to the vast numbers of small species of, e.g., the rodent and bat orders. Moreover, small mammals would need to be trapped and, in many cases, killed and dissected to ascertain their species identity – procedures not without ethical concerns that also require special permits. In comparison, the species identity of larger mammals can be gleaned by looking at them or studying their photo and film images. Names of larger animals are also engrained in local knowledge and can easily be double-checked with the help of guide books.

The findings about the existence and abundance of large mammals allows to relate them to socioecological features of the specific study mammals – primates. Direct connections between non-primate mammals and primates occur, for example, because certain ungulates are preyed upon by baboons while others are not (Sommer *et al*. 2016; see *Ch. 07*); because putty-nosed and mona monkeys adjust travel in relation to predation risk by leopards (Arnold & Zuberbühler 2006, Arnold *et al.* 2011); or, similarly, because chimpanzees may select certain sleeping sites to minimize encounters with leopards (Fowler 2006).

Apart from its scientific value, such background information can aid strategies to conserve the national park (see *Ch. 07*) given that politics and the public (rather unfairly) pay more attention to "charismatic" or "iconic" animals, than to small critters (Feldhamer *et al.* 2003).

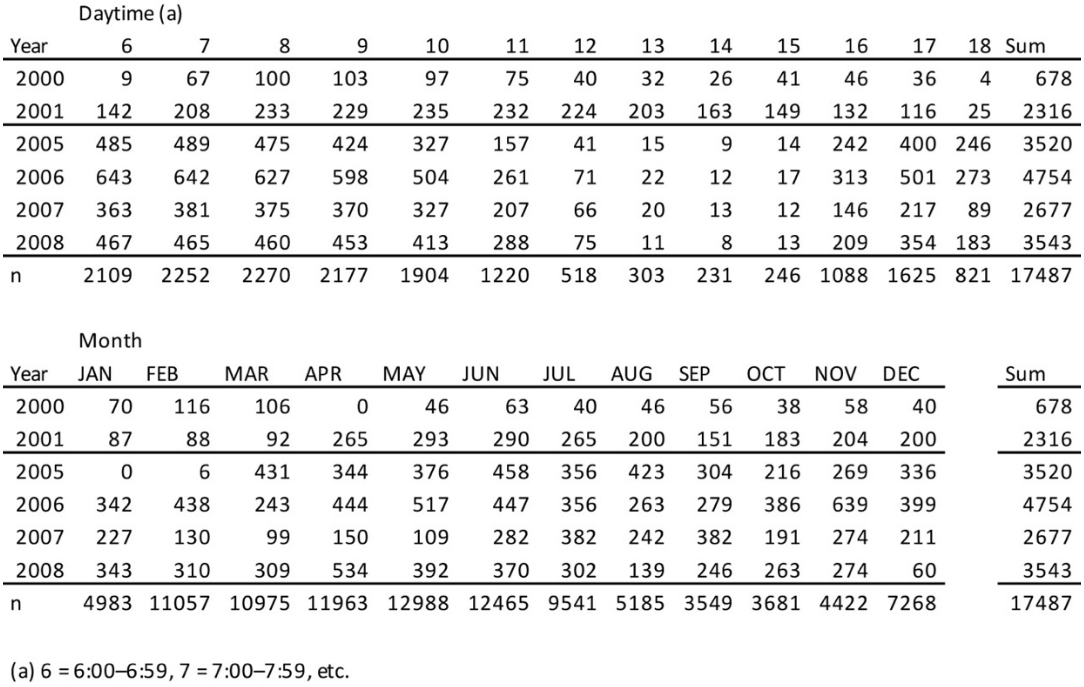
Survey Methods

Unaided visual records of large mammals in forested or fairly densely treed savannah-woodland habitats are very hard to come by, as these animals are shy, elusive, rare or nocturnal – a situation very unlike the more accessible observations of herbivores and carnivores in the vast grassy plains such as, e.g., the Serengeti in Tanzania. Nevertheless, GPP's research amassed thousands of direct sightings of Gashaka-area mammals via systematic foots surveys, chance observations and camera traps. These devices ~~are~~ have been used for wildlife research since the 1920s (Chapman 1927, Kucera & Barret 2011), as they enable records of elusive animals and can be employed to track their movements (Keeping & Pelletier 2014). Such cameras, capturing still or video images, have recently become widely popular – not least, because the respective technology became much cheaper and image quality much more sophisticated (Carbone *et al.* 2001, Srbek-Araujo & Chiarello 2005). They allow for higher species detection rates than reliance on indirect signs such as dung or footprints, enable continuous data collection during day *and* night, can detect very crepuscular species, and identify rare taxa with high certainty (Klailova *et al.* 2013). Camera traps are often strategically placed, e.g., at waterholes or – as done at Gashaka – at frequently trafficked animal trails, near bee or ant nests which apes exploit for honey or imagos, or at mineral licks. While such traps are perceived as "non-invasive", animals do, in fact, often react to the camera, given coloured control lights, mechanical sounds, or smell lingering on from humans who installed them. These cues may lead the animals to avoid the cameras, or, alternatively, to look straight at them, which – somewhat ironically – results in "better" pictures (Havercamp 2017).

The methods portfolio was as follows:

(i) *Foot surveys.* Field assistants and researchers recorded sightings of large mammals in the wider Kwano study area during a total of 17,487 h (*Tab. 02.02*). In terms of a statistical day – which lasts from 05:30–18:30, i.e. for 13 h –, this corresponded to (17,487 / 13 =) 1,345 statistical days. Thus, teams invested a cumulative total of (1,345 / 365 =) 3.7 years of survey time. The data were generated from 2001–2002 (2,994 h) and, in a more detailed fashion, from 2005–2008 (14,493 h). The second period thus translates into a very dense observation frequency of 3,623 h / year or 9.9 h / day.

Tab. 02.02. Time spent in the Kwano study area surveying large mammals by field assistants and researchers (2000–2001, 2005–2008). Single workers or teams carried out surveys. Number of hours based on the durations of individual surveys, not the size of teams



	Daytime (a)													
Year	6	7	8	9	10	11	12	13	14	15	16	17	18	Sum
2000	9	67	100	103	97	75	40	32	26	41	46	36	4	678
2001	142	208	233	229	235	232	224	203	163	149	132	116	25	2316
2005	485	489	475	424	327	157	41	15	9	14	242	400	246	3520
2006	643	642	627	598	504	261	71	22	12	17	313	501	273	4754
2007	363	381	375	370	327	207	66	20	13	12	146	217	89	2677
2008	467	465	460	453	413	288	75	11	8	13	209	354	183	3543
n	2109	2252	2270	2177	1904	1220	518	303	231	246	1088	1625	821	17487

	Month												
Year	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	Sum
2000	70	116	106	0	46	63	40	46	56	38	58	40	678
2001	87	88	92	265	293	290	265	200	151	183	204	200	2316
2005	0	6	431	344	376	458	356	423	304	216	269	336	3520
2006	342	438	243	444	517	447	356	263	279	386	639	399	4754
2007	227	130	99	150	109	282	382	242	382	191	274	211	2677
2008	343	310	309	534	392	370	302	139	246	263	274	60	3543
n	4983	11057	10975	11963	12988	12465	9541	5185	3549	3681	4422	7268	17487

(a) 6 = 6:00–6:59, 7 = 7:00–7:59, etc.

For these foot surveys, typically a single observer (and sometimes teams of 2–3 individuals) went on predetermined routes that systematically covered 1 x 1 km quadrants of the about 30 km^2 Kwano study area. The observers would adhere to a rota of walking and pausing to record sightings of pigs, antelopes and primates but also collected anecdotal information on other taxa. Surveys encompassed all months of the year and all hours of the daytime. Sightings (aka encounters) were converted into single data points covering a 30-min interval. For example, if pigs were seen to rummage in undergrowth between 11:57–12:15, this 18-min long sighting counted as a single entry for the daytime hour of 11:00-11:59. The total numbers of sightings per hour were corrected for diurnal and annual distribution of survey times, i.e. converted into rates / survey hour.

(ii) *Still-camera traps*. The foot-survey data are supplemented for some taxa (e.g., giant forest hog, bushbuck, yellow-backed duiker) through records from camera traps. These traps were first employed in the Kwano study area by GJ from 2011 onwards, generating still-photos. In particular, cameras were placed in front of mineral licks animals were likely to visit.

(iii) *Video-camera traps*. Counts for some rarely seen animals (e.g., blue duiker) are based on opportunistic records from 20 video-camera traps placed across the wider Kwano habitat for 3 years (2012–2014). These camera-trap efforts were coordinated by volunteer Anthony Agbor as part of "PanAf" (*Pan African Programme: The Cultured Chimpanzee*) initiated by the Max-Planck-Institute for Evolutionary Anthropology, Leipzig, Germany, and have already spawned various publications (Kühl *et al.* 2016, Havercamp 2017, Tagg *et al.* 2018).

(iv) *Monkey group counts*. Some data on putty-nosed, mona and colobus monkeys reflect systematic group counts in the Kwano study area along a standardised 9.5 km route, with observation time evenly spread across the daytime, executed by then-PhD student Jeremiah Adanu, over an 8-month period (2000).

(v) *Long-term data*. Numerical data for Kwano chimpanzees and baboons of both the Kwano and Gamgam study troops are based on other, more systematised protocols of long-term data collection (see *Ch. 04–06*).

The mixed portfolio of survey methods is not without *methodological constraints*. Firstly, the records do not rely on straight-line transect counts nor on grids. Thus, figures for abundance or detailed spatial distribution of particular species in the habitat could not be generated. (Line transect counts were only conducted from 2012–2014 as part of "PanAf", but data are not yet analysed.) Secondly, survey entries during successive days might capture the same individual animals or groups, resulting in an unknown number of "double-counts". Similar problems exist for still- or video-camera traps, in that it is difficult to distinguish between individuals (Klailova *et al.* 2013).

However, as resultant figures will often rely on compilations of records obtained from across a large area (about 30 km^2), double-counts are unlikely to swamp the overall outcome. Moreover, group sizes calculated from camera trap images and foot surveys turned out to be very similar. Finally, as has already been mentioned, these restrictions do not necessarily apply to the two main study primates, baboons and chimpanzees, for which much more detailed information is available (see *Ch. 04-06*).

Large Animals at Gashaka

Main Taxa

The longitudinal research in the Gashaka biome established that it is inhabited by about 50 or so species of large animals (excluding birds and fish), of which 40 are large mammals (*Tab. 02.03).*

Tab. 02.03. Notes on the status of main large animals in the Gashaka area of Gashaka Gumti National Park.

Taxon	Common name (a)	Latin name	Hausa name	Sightings (b)	Captured by camera trap
Primates	Chimpanzee	*Pan troglodytes ellioti (*aka *vellerosus)*	Biri mai ganga	C	x
	Olive baboon	*Papio anubis*	Gogo	C	x
	Putty-nosed monkey	*Cercopithecus nictitans*	Bakinbiri	C	x
	Mona monkey	*Cercopithecus mona*	Gimchiki	C	x
	Tantalus monkey	*Cercopithecus aethiops*	Kirikaa	O	
	Patas monkey	*Erythrocebus patas*	Jambiri	(c)	
	Black-and-white colobus	*Colobus guereza*	Biri mai roro	C	x
	Grey-cheeked mangabey	*Lophocebus albigena*		R (d)	
	Milne-Edwards potto (N)	*Perodicticus edwardsi*		R	
	Galago (N)	*Galago spp.*		R	
Scaly ant-eaters	Tree pangolin (N)	*Phataginus tricuspis*	Dankunya	R	x
Hares	Scrub hare	*Lepus saxatilis*	Zomo	R	
Rodents	Derby's flying-squirrel	*Anomalurus derbianus*	Kurege	R	
	Gambian sun-squirrel	*Heliosciurus gambianus*	Kurege	C	
	Brush-tailed porcupine (N)	*Atherurus africanus*	Beguwa	O	x
	Crested porcupine (N)	*Hystrix cristata*	Beguwa	O	x
	Gambian giant rat (N)	*Cricetomys gambianus*		Probably present	
	Marsh cane-rat	*Thryonomys swinderianus*	Jebji	C	
	Savannah cane-rat	*Thryonomys gregorianus*	Jebji	C	
Aardvarks	Aardvark (N)	*Orycteropus afer*	Dubganya	C (burrows)	x
Hyraxes	Rock hyrax	*Procavia ruficeps*	Agwada	O	
Ungulates	Red river hog	*Potamochoerus porcus*	Jan alde	O	x
	Warthog	*Phacochoerus africanus*	Alden daji/Alhanzir	O (at Gashaka, 10 km away)	
	Giant forest hog	*Hylochoerus meinertzhageni*	Bakin alde	O	x
	African buffalo	*Syncerus caffer*	Bauna	O	x
	Bushbuck	*Tragelaphus scriptus*	Mazo	O	x
	Waterbuck	*Kobus ellipsiprymnus*	Gwombaza	O	x
	Hartebeest	*Alcelaphus buselaphus*	Kanki	O	
	Yellow-backed duiker	*Cephalophus silvicultor*	Boka	O	x
	Blue duiker	*Cephalophus monticola*	Gada	O	x
	Red-flanked duiker	*Cephalophus rufilatus*	Makurna	O	x
Carnivores	Long-snouted mongoose	*Herpestes naso*	Munzuru	R	x
	Spot-necked otter	*Lutra maculicollis*	Karenruwa	R	
	African civet (N)	*Civetticus civetta*	Tunkun juda	O	x
	Genet	*Genetta sp.*	Tunku	R	x
	Golden cat	*Felis aurata*	Kawondamisa	R	x
	Leopard	*Panthera pardus*	Damisa	R (also heard, scratch marks)	
	Wild dog (c)	*Lycaon pictus*	Kerkeshi/ Karendaji	R	
	Honey badger	*Mellivora capensis*		R	x
	Lion (c)	*Panthera leo*	Zaki	R (seen at Yakuba, 15 km	
	Side-striped jackal	*Canis adustus*	Dila	O (seen at Selbe, 15 km away)	
	Spotted hyena (c)	*Crocuta crocuta*	Kura	R (heard at Selbe, 15 km away)	
Reptiles	Nile monitor lizard	*Varanus niloticus*	Guza	R	x
	Nile crocodile (c)	*Crocodylus niloticus*	Kada	R	
	Rock python	*Python sebae*		O	
	Cobra	*Naja sp.*		O	
Birds	(e)				

(a) N = predominantly active during the night
(b) Actual sightings by fieldworkers only; C = common, O = occasional, R = rare
(c) Not at Kwano but in surrounding area (< 20 km distance) (Kamayah et al. 2003)
(d) Since 2005 (K. Arnold pers. comm.; V. Sommer pers. obs.)
(e) 431+ species identified in Gashaka Gumti National Park (see, e.g., Dunn 1999)

The prominent taxa include carnivores (African civet, golden cat, leopard – with occasional incursions of hyena, lion, wild dog from the flat grasslands of Gumti sector), ungulates (red river hog, giant forest hog, African buffalo, bushbuck, red-flanked duiker, yellow-backed duiker, waterbuck), rodents (crested porcupine), pangolins, and aardvarks. The forest-savannah-mosaic also harbours 10 species of primates, with two nocturnal species, and diurnal taxa including chimpanzee, baboon, putty-nosed monkey, mona monkey, black-and-white colobus monkey, tantalus monkey. Patas monkeys occur in grassy and flat biomes. There have also been isolated sightings of Grey-cheeked mangabeys . It is worth mentioning that gorillas have been rumoured to occur, too. Initially based on amateurish assumptions (White 1990), these claims are not completely unreasonable, as remnant populations of *Gorilla gorilla diehli* are found not so far to the south-west (Caldecott & Miles 2005). However, several large-scale GPP expeditions into unexplored forests around Mount Gangirwal (2005, 2006, 2007, 2014, 2018) were as yet unable to discover any evidence for the presence of gorillas in GGNP.

Thus, GGNP represents one of the last areas in West- and Central Africa where a large assemblage of wildlife still survives. Still, in the past, there has been no photographic evidence of many of even the most iconic animals that inhabit GGNP. However, with long-term research and the advent of camera traps, this has changed – as shown by the tableaux of images in *Fig. 02.09*. Several of these photos represent "firsts", such as the pictures of blue duiker, aardvark, genet, golden cat and honey-badger. The park's diurnal non-human primates can be photographed much more easily. As for the nocturnal primates, only a single image of a wild-living potto exists, and none of a galago (*Fig. 02.10*).

The only eminent large mammal that has not been photographed so far and has not been caught with a camera trap, is the *leopard*. Apart from humans, leopards are probably the most important threat for monkeys and apes, with corresponding effects on their patterns of sociality. Despite a lack of images, indirect evidence (scats, footprints, vocalizations, scratch-marks, anecdotes about predation and hunting) establishes beyond doubt that these carnivores still exist in the Gashaka-Kwano area, and indeed other forested parts of the park (*Tab. 02.04*). Leopards loom large in local narratives, several of which have been reconstructed via interviews, and these cats have also been met by people walking the forest at close range – including by me.


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Fig. 02.09. Examples of large animals inhabiting the Kwano area. Most images represent first-time visual records for the region. Captured by still-camera (photographer noted), video-camera traps by Anthony Agbor (VT-AA) or still-camera traps by Gonçalo Jesus (SC-GJ). (Photos: © GPP, (a) Red river hog (*Potamochoerus porcus*), VT-AA, (b) Warthog (*Phacochoerus africanus*), David Bennett, (c) Giant forest hog (*Hylochoeros meinertzhageni*), VT-AA, (d) African buffalo (Syncerus caffer), VT-AA, (e) Bushbuck (*Tragelaphus scriptus*), SC-GJ), (f) Waterbuck (*Kobus ellipsiprymnus*), David Bennett, (g) Yellow-backed duiker (*Cephalophus silvicultor*), SC-GJ, (h) Blue duiker (*Cephalophus monticola*), VT-AA, (i) Red-flanked duiker (*Cephalophus rufilatus*) VT-AA (j) Tree pangolin (*Phataginus tricupsis*), Andrew Fowler, (k) Crested porcupine (*Hystrix cristata*), SC-GJ, (l) Aardvark (*Orycteropus afer*), VT-AA, (m) Rock hyrax (*Procavia ruficeps*), David Inglis, (n) Spot-necked otter (*Lutra maculicollis*), Sandra Tranquilli, (o) African civet (*Civetticus civetta*), VT-AA, (p) Genet (*Genetta sp.*), VT-AA, (q) Golden cat (*Felis aurata*), VT-AA, (r) Honey-badger (*Mellivora capensis*), VT-AA, (s) Nile crocodile (*Crocodylus niloticus*), Umaru Buba, (t) Rock python (*Python sebae*), Samara Albuquerque)

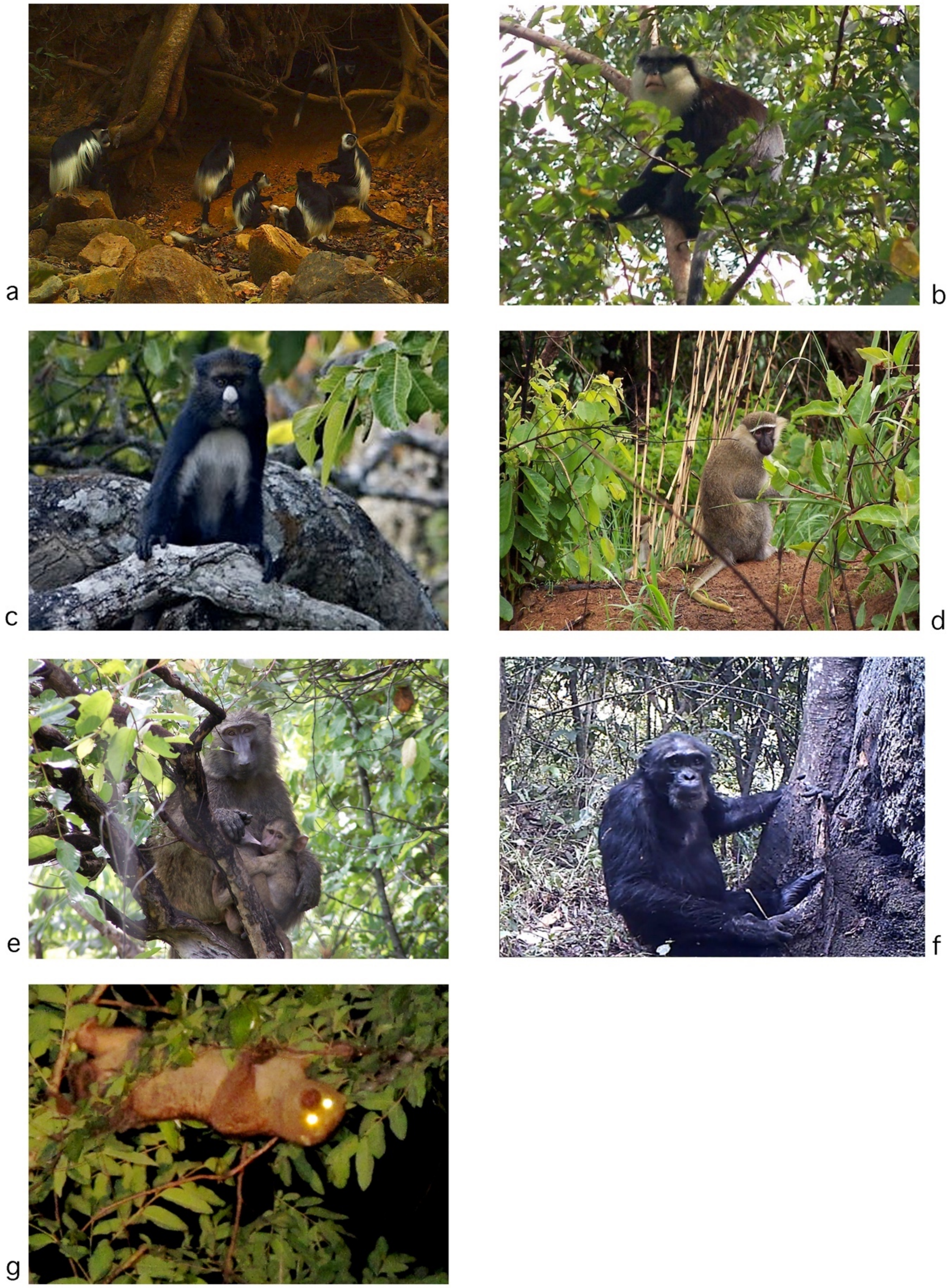

Fig. 02.10. Non-human primates inhabiting the Kwano area. (a) Black-and-white colobus (*Colobus guereza*), (b) Mona monkey (*Cercopithecus mona*), (c) Putty-nosed monkey (*Cercopithecus nictitans*), (d) Tantalus monkey (*Cercopithecus aethiops*), (e) Olive baboon (*Papio anubis*), (f) Chimpanzee (*Pan troglodytes ellioti*), (g) Milne-Edwards potto (*Perodicticus edwardsi*). (Photos: © GPP, GJ [a, g], Tabitha Price [b, c], David Benett [d], Alejandra Pascual-Garrido [e], Anthony Agbor [f]

Tab. 02.04. Leopards in Gashaka Gumti National Park: sightings and local narratives

Evidence	Date	Description	Location	Informant (a)
Scats	2009	Leopard scats found during survey	Gumti sector of national park	(b)
Predation	2008	"Fulani people say leopard ate a cow calf; they say leopard is sometimes coming close to their home stead"	Near Chappal Tale	HG
	2009	"Found red-flanked duiker with eaten back leg and bite marks neck. It was hidden under tree and covered with leaves. The next day it was gone"	1 km from Kwano, trail N11	HI (with MSc student Gemma Price)
		"There are no reports that leopards have attacked people"		HG
Footprints	2005	1 footprint	1 km from Kwano, Transect A760	HG, with PhD researcher Andrew Fowler
	2008	Foot prints	Near Kwano at Mayo Dim	HI
	2006 Mar	1 large footprint	Gangirwal forests, near last waterfall up from Gamgam trail	Volker Sommer and others
	2009 Feb	3 footprints on buffalo trail	1 km from Kwano, forest of finger 3	HG
	2009 Sep	Many footprints	Near Kwano, from FP180 to end of FPxR	HG
Growls	1999–2000	Heard	Near Kwano	Isabelle Faucher, PhD researcher
	2008 rainy season	"Many growls in forest" (19:00)	3 km from Kwano, FP60	HG, HI
Scratchmarks	1999–2000	Saw marks	Near Kwano	Isabelle Faucher, PhD researcher
	2008	Saw marks in an *Uapaca* tree	1 km from Kwano, trail V	HI
		Never saw scratchmarks		HG
Sighting	1993	Saw female	Between Gashaka and Serti	HI, with Buba Bello
	2000, earliest	Saw leopard	Chappal Hendu	BB
	2006 Jan	Saw leopard (or other large cat?)	1 km from Kwano , FP170	Volker Gallitz jun, German engineer
	2009 Feb	Saw leopard close-up on research trail	1 km from Kwano, between trails N and D, ca 30 m from main footpath	Gonçalo Jesus
	2009, rainy season	"A man told he had seen a leopard. The man ran away."	Close to Kwano	HI
	2012–14	Not caught on ca 50 camera traps	Kwano habitat	Gonçalo Jesus
Poaching	1989 ca	"Sule of Kwano village caught a leopard in a snare, and sold skin to Wakili of Gashaka, who sold it on"		HG
	1991, before	"Before area was national park, people used to come buy skins, which are liked by big man"		HG
	1991, before	"One man, now dead, used to deal in leopard skins"	Serti	HG
	1997 ca	"Man caught leopard in snare. He tried to shoot it, hit the wire. The leopard attacked his face, broke his eye-socket towards ear; they carried him to Cameroon for treatment"	Near Flinga in bush	HG
	2003 ca	"Park rangers arrested a man near Gashaka who carried a skin from Cameroon to Serti"	Near Gashaka	HG

(a) Local field assistants, interviewed Mar2010: HG = Hammaunde Guruza, BB = Bobbo Buba, HI = Halidu Ilyasu

(b) Saidu, Yohanna; Philipp Henschel, Guy Balme, Andrew Dunn (2010).

Mammal Group Sizes

Apart from such qualitative accounts, the long-term research generated quantitative data for several large mammal species about the likelihood, with which they are spotted during surveys, and associated factors such as numbers of animals seen together. These are detailed in *Tab. 02.05.*

Tab. 02.05. Group sizes of mammals (antelopes, pigs, carnivores, primates) most commonly encountered in the Kwano study area. Sightings include an unknown number of double-counts. For Latin names see *Tab. 02.03.*

Taxon	Common name	Sightings	Mean	Min	Max	SD	HB (cm) (b)	W kg (b)	Infants seen?	Remark (a)
Antelopes	African buffalo	29	5,8	1	12	3,2	225–340	425–850	Y	2005-2008 habitat survey
	Waterbuck	397	3,0	1	8	1,4	175–235	160–300		2005-2008 habitat survey
	Bushbuck	65	1,3	1	2	0,5	114–150	24–60	Y	2005-2008 habitat survey
		134	1,6	1	3	0,4				Still-camera trap at mineral lick
	Yellow-backed duiker	129	1,1	1	2	0,6	125–190	45–80		2005-2008 habitat survey
		15	1,0	1	1	0,0				Still-camera trap at mineral lick
	Red-flanked duiker	40	1,1	1	2	0,3	60–80	6–14		2005-2008 habitat survey
	Blue duiker	5	1,6	1	2	0,5	55–90	3.6–9		2012–2014 video-camera trap
	Hartebeest	5	3,0	1	8	2,9	160–210	116–218	Y	2005-2008 habitat survey
Pigs	Red river hog	271	5,3	1	13	2,1	100–145	45–115	Y	2005-2008 habitat survey
	Giant forest hog	16	3,8	1	11	3,0	130–210	100–275	Y	2005-2008 habitat survey
		20	4,5	1	11	3,0			Y	Still-camera trap at mineral lick
Carnivores	Spot-necked otter	3	1,7	1	2		60–65	4–7		Various observers, 2000-2009
	African civet		ca. 1.5	1	2		68–95	7–20		At times seen daily at research station garbage dump
	Leopard	3	1,0	1	1		104–190	28–60		3 observers, 1993, 2008, 2009
	Golden cat	1	1,0	1	1		61–102	6–18		2005-2008 habitat survey
		4	1,0	1	1					2012–2014 video-camera trap
	Genet	5	1,2	1	3				Y	2005-2008 habitat survey
Primates	Chimpanzee	306	4,0	1	21	2,6	64–90	26–40	Y	Total size of Kwano community estimated about 30 (Sommer et al. 2004)
	Olive baboon	7	22,3			6,5	50–114	11–50	Y	Dedicated group counts, Higham et al. 2009
	Putty-nosed monkey	54	20,9	1	34	6,5	40–57	3–10	Y	Dedicated group counts by Jeremiah Adanu, May-Dec00
	Mona monkey	46	15,0	1	30	6,3	34–63	2–6	Y	Dedicated group counts by Jeremiah Adanu, May-Dec00
	Tantalus monkey	92	6,0	1	19	3,3	38–83	3–9	Y	2005-2008 habitat survey
	Black-and-white colobus	45	10,7	1	15	2,2	48–70	5–14	Y	Dedicated group counts by Jeremiah Adanu, May-Dec00
		12	2,3	1	6	2,0				Still-camera trap at mineral lick
	Milne-Edwards potto	1	1,0	1	1		30–40	0.8–1.6		Seen once close to Kwano field-station

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(a) All data based on opportunistic counts during habitat surveys, 2005–2008, if not stated otherwise

(b) HB = head and body, W = weight; source: Kingdon 2014

As for group sizes, monkeys are clearly the most gregarious large mammals, with averages of 6–22 animals per group. The two types of forest pigs are the next most sociable (4–5 animals per group). Antelope species encompass a greater variation of group sizes, from buffalos with an average of 6 animals, via waterbucks and hartebeests with 3 animals, while smaller antelopes such as bushbuck and duiker are typically solitary. Carnivores are likewise mostly solitary, even though pairs are not uncommon.

Chimpanzees occupy a special place with respect to group sizes, given their fusion-fission pattern, because only a fraction of the whole community is sighted at one time – an average of 4 animals in the case of the Kwano study area.

Foot Surveys of Ungulates

During the 2005–2008 foot surveys in the Kwano habitat, observers recorded 956 sightings for 9 species of ungulates (cf. *Tab. 02.05*). Data for three species were too scarce to be analysed (giant forest hog, 1.7 %; hartebeest, 0.5 %; blue duiker, 0.4 %). The quantitative results presented in the following are therefore restricted to the 6 most commonly observed species, which constitute 97.4 % of all encounters (water buck, 41.5 %; red river hog, 28.3 %; yellow-backed duiker, 13.5 %; bushbuck, 6.8 %; red–flanked duiker 4.2 %; buffalo, 3.0 %).

Each of these six species was met during each month of the year. They were also encountered during virtually every hour of the daytime, although there is a spike during the penultimate daytime hour and a noticeable lull around noon (the latter likely caused by low observation effort, cf. *Tab. 02.02*).

A corresponding lack of seasonal variation is also apparent if one calculates the mean numbers of animals per encounter. As for variation throughout the year, only buffalo group sizes vary considerably (perhaps due to stochastic effects of small sample size). Group sizes do also not fluctuate much during the daytime, again except for a decrease around the hottest hours of the day for buffalo, waterbuck and red river hog.

As for the range of group sizes, three antelopes are found to be mostly solitary (bushbuck, yellow-backed duiker, red-flanked duiker). Numbers of waterbuck average 3, with a range of 1–8, while buffalos average 6, with a range of 1–12. Similarly, red river hog average 5 animals per sighting, with a range of 1–13 (*Fig. 02.11*).

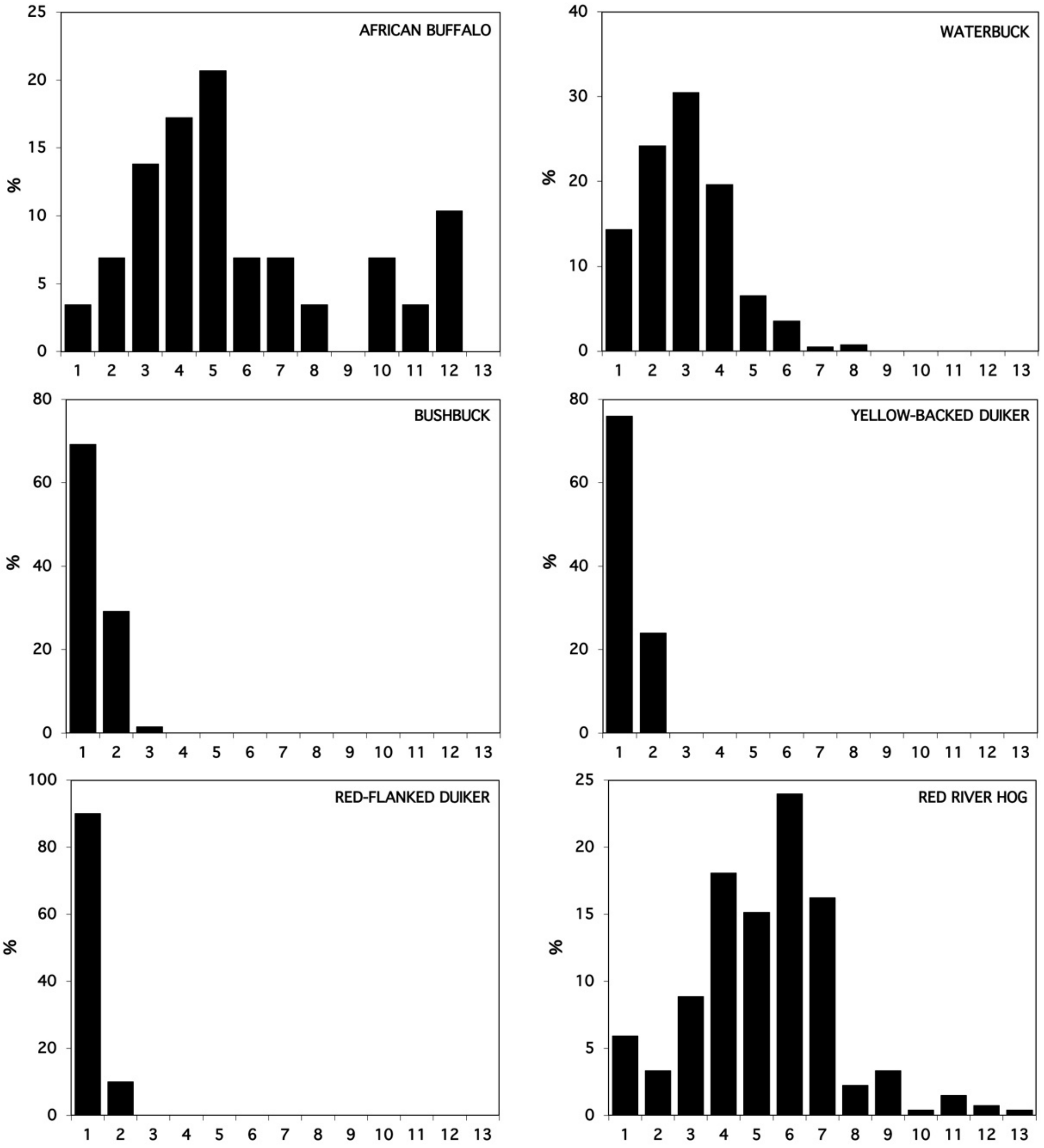

Fig. 02.11. Group sizes of antelopes and pigs. Based on opportunistic sightings during 2005–2008 surveys. Details in *Tab. 02.05*

Sightings in different vegetation types of the study area (controlled for patch size, i.e. 27.8 % savannah, 77.2 % forest) indicate that only red river hog were more often met in closed habitat, while at least three quarters of waterbuck, buffalo and bushbuck encounters occurred in open terrain (*Fig. 02.12a*). Sightings comparing wet vs. dry season were rather balanced (*Fig. 02.12b*).

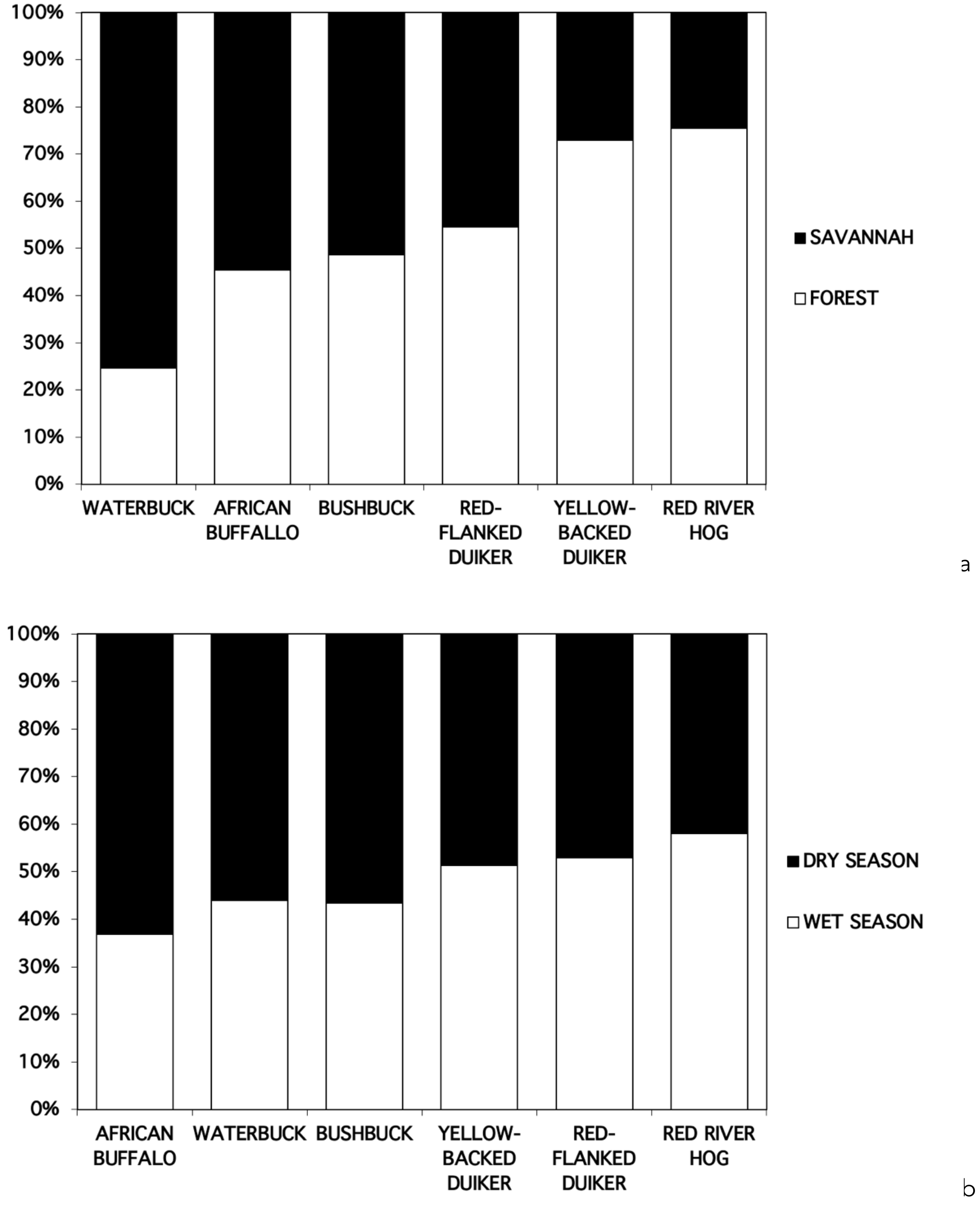

Fig. 02.12. Habitat variables influencing the likelihood of sightings of antelopes and pigs. (a) Savannah versus forest patches. (b) Wet season (Apr–Oct) versus dry season (Nov–Mar)

Foot Surveys of Monkeys

The 2005–2008 foot surveys in the Kwano habitat also recorded monkey sightings. These data are more easily generated than those for ungulates, given that monkeys, due to their largely arboreal nature, are readily observable while walking through the habitat.

The quantitative results presented in the following are based on 600 sightings of the five types of monkey at the Kwano study site. Compared to ungulates, monkey species did not differ as dramatically with respect to the proportion of sightings (baboons, 27.0 %; putty-nosed monkey, 23.8 %; colobus, 22.7 %; tantalus monkey, 15.3 %; mona monkey, 11.2 %).

These data suggest that tantalus and mona monkeys are less abundant. This is certainly true for tantalus, as they are only found in a small part of the survey area, i.e. some more open savannah parts in the west. A very different picture would have emerged, if one would have used the same survey methods at the Gamgam study site, as here, more terrestrial monkeys such as tantalus and baboons are more common than more arboreal forms such as colobus and putty-nosed.

All monkey species are met throughout the year, with very little variation between months, and all are also seen during virtually every daylight hour. However, similar to ungulates, encounter rates markedly decrease towards midday (with a lull from 14:00-15:00 h), followed by a dramatic peak from 16:00 h onwards.

Again, as for ungulates, mean numbers of animals per sighting do hardly vary throughout the year, while diurnal fluctuations in values are more noticeable.

While ungulate group sizes (cf. *Fig. 02.09*) were calculated from foot survey data, those for monkeys rely on dedicated counts of particular groups (cf. *Tab. 02.05*). The average number of sighted animals is generally much larger for monkeys than for ungulates (*Fig. 02.13*), including values for maximum group sizes: baboons, 20; putty-nosed monkey, 34; colobus, 15; tantalus monkey, 19; mona monkey, 30).

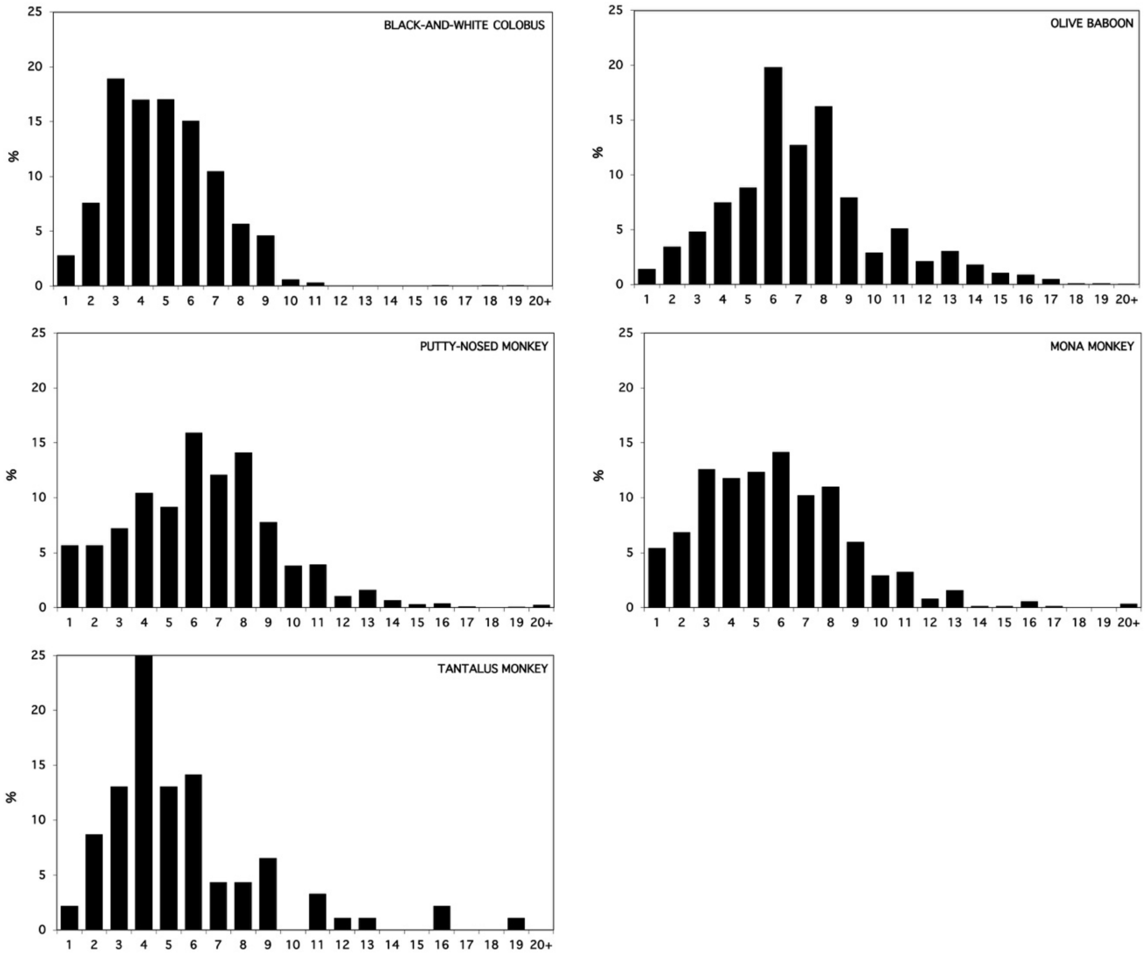

Fig. 02.13. Group sizes of monkeys. Unlike other data, these figures reflect dedicated counts during 740 h of systematic survey walks conducted from May–Dec 2000, spread out evenly from 07:00–19:00 over 9.5 km of non-random, marked forest trails (Jeremiah Adanu, unpubl. data, analysed by GJ)

Mammalian Gregariousness

This research aimed to obtain data on wildlife abundance at Gashaka, and, failing that, at least about presence or absence of certain taxa. Like researchers elsewhere, various methods were employed (foot surveys, camera traps, track surveys), but all of these have limitations (e.g., double counting, under- or over-estimation, biases towards conspicuous animals; Cook & Jacobson 1979, Seber 1992, Silveira *et al.* 2003). It is even more difficult to understand the dynamics of within-species grouping, i.e. gregariousness. Group sizes often vary wildly within and between populations and between different seasons. This is due to diverse selection pressures, including intragroup and intergroup competition for shelter, food and mates, travel costs, risks of predation and transmittable diseases, benefits through cooperation and safety in numbers, all coupled with seasonal effects (review for mammals in Clutton-Brock 2016). Moreover, wildlife abundance and animal behaviour may also be influenced by human hunting practices (Woodroffe & Ginsberg 1998, Harrison 2011). In the Gashaka area, with the inception of the *Gashaka Primate Project*, hunting has dramatically declined; for example, around Kwano, for more than a decade, not a single wire snare has been found.

Only anecdotal evidence about the general biology of rather solitary or pair-living species, e.g., pangolins, hares, rodents, aardvarks, carnivores, duikers was gathered (cf. *Tab. 02.03*, *Fig. 02.07*, *Tab. 02.05*). In contrast, a reasonable set of quantitative data was collected on six mostly large ungulate species. The likelihood that surveyors encountered these taxa varied considerably, a fact for which a variety of explanations can be furnished.

The most commonly seen mammal, the waterbuck, is particularly large and essentially savannah-dwelling, which allows for the detection of this animal from afar, even while it flees from observers. The species detected second most often, red river hog, is conspicuously coloured, travels in relatively large groups and is often noisy, thus drawing the attention of the surveyors into their direction.

Encounter frequencies for the major ungulates decreased around noon – likely reflecting restricted animal movement during the hottest hours –, and increased just before nightfall – probably echoing a last bout of foraging to store energy for the night as well as movements towards preferred sleeping sites.

The mean number of individuals seen together was more or less constant throughout the year. This is related to the fact that the study ungulates did not constitute large anonymous "herds" – like those forming in the Serengeti in response to fluctuations of resource availability (McNaugthon 1983) –, but individualised kin-groups or reproductive units.

Open versus closed habitat seemed to have a considerable influence on recorded encounters at Kwano. The dramatic preponderance of waterbuck, buffalo and bushbuck sightings in open savannah as compared to forest (cf. *Fig. 02.12a*) may reflect a habitat preference on behalf of the animals. However, it is also likely that field assistants can spot them more easily in open landscape, given that three quarters (73.2 %) of all sightings were ungulates in savannah. The assumption is supported by the fact that sightings were less common during the wet season (43.3 %) when high grass is sprouting in the savannah – which in turn reduces the likelihood to see savannah-dwelling animals. This then reduces the asymmetry between animals preferentially encountered in forest vs. in the savannah, and leads to rather balanced proportions for the different seasons (cf. *Fig. 02.12b*). Another contributing factor might be that observers are less noticeable in forests during the wet season, because rainfall often provides background noise and as the ground is moist, the sound of footsteps is buffered.

In contrast to some non-primate mammals, sightings of primates are certainly very common here. The Kwano study area has been nicknamed "a primate paradise"; Sommer & Ross 2011). Without much effort, groups of arboreal mona monkeys, putty-nosed monkeys, black-and-white colobus as well as semi-terrestrial baboons can be readily observed. Tantalus monkeys are also readily spotted, although less often at Kwano than at the Gamgam study site with its adjacent agricultural fields near the villages of Gashaka.

Surveyors saw monkeys more often during the early mornings and late afternoons, which coincides with movements out and towards sleeping sites as well as first and last foraging bouts. Recorded group sizes fluctuate little throughout the year, reflecting the tight sociality of monkey groups, which, in relation to overall numbers, experience comparably few demographic events such as immigration, emigration or births.

Gashaka as a Mammalian Refuge

Gashaka Gumti National Park was created, not least, because of its abundant wildlife (Barnwell 2011). Still, over the last two decades, some of its most iconic big animals – lion, hyena, wild dog, elephant, probably also giant eland – went extinct, largely as a result of Fulani cattle herders poisoning and killing them in the northern and flat Gumti sector of the park (Saidu *et al.* 2010). Moreover, the pan-African rinderpest in 1983–84 killed thousands of ungulates in the park, and populations may still not have entirely recovered (Dunn 1993). Additional pressure comes from hunters who extract bush-meat (Nyanganji *et al.* 2011).

The situation in the mountainous southern Gashaka sector of the park is not as dire. The Kwano study site in particular still hosts what is likely a full original assemblage of large mammals (cf. *Tab. 02.03*, *Fig. 02.09*, *Fig. 02.10*), a positive situation for which the *Gashaka Primate Project* can claim much credit (for the effect of research projects on conservation, see Tranquilli *et al.* 2014). Still, knowledge even about larger mammals is still spotty. Prosimians in particular have not been properly surveyed, and it may well be that more taxa exist then just Milne-Edwards potto and perhaps two galagos – believed to be Senegal Galago (*Galago senegalensis*) and Thomas's Dwarf Galago (*Galagoides thomasi*), Dunn 1999).

The Gashaka sector may be the last significant refuge for carnivores such as golden cat and leopards. Evidence for the presence of leopards is continuous throughout decades, albeit rare (cf. *Tab. 02.04*). This is in line with the fact that these felids are solitary hunters with home ranges that can exceed 100 km^2 (Kingdon *et al.* 2013). Unlike in other parts of Africa or India, no reports exist of leopard attacks on people in GGNP, perhaps because leopards have learned to avoid humans due to traditional hunting pressure. Many behavioural and grouping features of mammals at Kwano are likely to reflect leopard predation risk, in particular also primate gregariousness (Miller 2000) – effects to which threats from other large predators can be added (crowned eagles, rock pythons, Nile crocodiles, golden cat).

In terms of the overall situation, the accumulated data amassed through longitudinal research by the *Gashaka Primate Project* and analysed by me established that the park is still one of the last remaining areas in West Africa that harbours a substantial assemblage of large mammals. Armed with this background information, the following chapters will explore the fine-grained dynamics of how ecological factors influence the gregariousness and reproduction of two primate focal species – chimpanzees and baboons (*Ch. 03-06*).

CHAPTER 03

SEASONALITY IN A SAVANNAH-FOREST MOSAIC.

CLIMATE AND PLANT PHENOLOGY

Fig. 03.01. Fruit specimens from forests and savannah near Kwano study site. *Cola gigantea* (red fruit in brown pod, top l.), *Tabernaemontana pachysiphon* (large brown and small green fruit, top r.), *Annona senegalensis* (speckled green fruit, middle l.), *Costus afer* (berries, middle centre), *Ficus spp.* (green fruit, bottom l.), *Afzelia africana* (white seed pod, bottom l.), *Irvingia spp.* (green and yellow fruit, middle l.), *Landolphia spp.* (orange fruit, middle centre), *Pseudospondias microcarpa* (single black fruit, bottom centre), *Pycnanthes angolensis* (single red fruit, bottom centre), *Leea guineensis* (orange flower and brown berries, bottom r.), *Strephonema mannii* (middle r.). (After Koutsioni & Sommer 2011: Fig. 5.1, with spellings corrected; photo: Volker Sommer)

INTRODUCTION

The behaviour and reproduction of animals will be constrained by the features of its habitat such as geophysical texture, climate and plant cover. The latter typically provides resources for shelter and food. Plants are likewise constrained by environmental factors, and the discipline of phenology investigates how their cyclic life events are influenced by climate and elevation (Osborne 2000).

Within this complex network, the cascade of impact (Van Schaik & Brockman 2005) starts with regional climates that, over a long course of time, shape the landscape's profile, mainly through the carving flow of water. This then affects the soil shield and its function as a medium for plant growth and the development of vegetation structures, from grassland to open scrubland with scarce woody vegetation to woodlands with scattered trees to closed rainforests with densely packed tall trees. The proximate production of plant cover will be influenced by annual resp. supra- or sub-annual cycles in rainfall (Adamescu *et al*. 2018). The timing of rain and available sunlight will in turn determine the succession of phenophases, i.e., leafing, flowering, and fruiting which govern the reproductive success of plants (ibid.). The cyclical biological events in the lives of plants will influence the animals that use vegetal resources by responding to the quantity, quality and distribution of potential items that provide food or protection (van Schaik *et al*. 1993). As for primates, numerous studies have concluded that their behavioural pattern, variation in social organization and demographic variables largely reflect the predictability of food resources, mainly fruit (Chapman *et al*. 2017).

However, compared to forests in Asia and the Neotropics, the phenology of African forests is not well understood (Adamescu *et al*. 2018). Main constraints are a great deal of variation in phenophases between and within habitats, and a general paucity of long-term datasets (ibid.).

Within this general framework, the following chapter provides detailed background information, much of it based on long-term research, about climatic patterns and corresponding changes to vegetation cover and fruit productivity of trees and vines in the Gashaka study area. Such material will prepare the ground for the goal of this research, i.e. linking primate sociality with habitat seasonality and ecology (*Fig.03.01*). The presentation of detailed quantitative reconstructions (see below) shall be preceded by the outlining of the main areas through and in which the phenological phenomena play out: climate, wildlife, tree cover, fruit production of trees and vines.

Climate

Near the equator, climatic seasonality is almost inexistent, and the further away one moves from latitude zero, the more seasonal the climate gets, with increased contrasts between wet and dry seasons. Rainfall coincides with, or follows the peaks of solar radiation, given that irradiation causes air to rise and cool down, which generates precipitation if the air is moist enough (van Schaik & Pfannes 2005). However, as a typical tropical feature, the temperature varies comparatively little across the seasonal trajectory – instead, the fluctuation in temperature over 24 hours is greater than the range of monthly means (Van Schaik & Brockman 2005).

North-eastern Nigeria is located at a latitude of 7 degrees north of the equator, where the northward movement of the intertropical convergence zone (ITCZ) causes heavy precipitation from Apr–Oct, with a peak between Jul–Sep (Cronin *et al.* 2014). When the ITCZ moves southwards, it creates a dry period from Nov–Mar that brings down dusty and dry "harmattan" winds from the Sahara (Oates *et al.* 2004, Cronin *et al.* 2014). The precise timings of the marked wet and dry seasons are expected to have major impact on both faunal and floral ecology.

Biodiversity

In general, the less harsh an environment is, the more diverse are its associated life forms – with moist tropical rain forests being regarded as a particularly species-diverse type of habitat.

The northern border of the Biafra forests and highlands, located in the nations of Cameroon and Nigeria, have been identified as a centre of biodiversity that includes high levels of endemism (Oates *et al.* 2004, Cronin *et al.* 2014). The Gashaka area lies just above this Guineo-Congolian moist zone (Bergl *et al.* 2007). Although not technically regarded as biodiversity hotspot, the location of Gashaka at the convergence between Guinea savannah (aka Guinean forest-savannah mosaic) and West African Guinean forests plus its mountainous nature with peak elevations of up to 2500 m (belonging to the Cameroonian Highlands forests ecoregion) has shaped the considerable diversity of flora and fauna in Gashaka Gumti National Park (Dunn 1999, Oates *et al.* 2004).

Savannah-Woodland

The park's Gashaka sector is comprised of a mosaic of habitat types, with semi-deciduous riverine, lowland and montane forests interspersed with savannah-woodland and montane grassland. The immediate Gamgam-Kwano study area consists of forests and savannah, interspersed with small patches of grassland.

The exact definition of what constitutes a savannah varies from source to source (Alberts *et al.* 2005). In general, savannahs are tropical biomes dominated by grasses, with drought-resistant trees and shrubs scattered across. Compared to temperate zone grasslands, savannahs experience less dramatic shutdown of plant productivity across the year – albeit the plant cover may still fluctuate considerably, as a result of seasonality in rainfall (ibid.)

In conjunction with climatic factors, the chequered vegetation cover of the study area is largely maintained through regular fires that burn the grass thriving in open landscape (Adanu *et al.* 2011). These fires are human-made, while natural fires like those caused by lightning are infrequent in comparison. Like elsewhere in Africa, grass is set ablaze with the belief that it controls outbreaks of invertebrates, creates better visibility and accessibility, or grazing pasture with ashes enriching the nutrient content of the soil. GGNP harbours thousands of heads of cattle in its enclave settlements, and pastoralists frequently drive herds through the reserve – which partly explains, that even in the national park, burning is a frequent occurrence (*ibid.)*.

In regularly burnt areas, savannah plants including trees exhibit adaptations to fire (Osborne 2000). This terrain is covered with graminaceous plants and sparse stands of short and fire-resistant trees. Succulent species are almost entirely absent, probably because they lack adaptations to fire (Pennington *et al.* 2009).

Rain Forests

In contrast to grass-covered open habitats, woody plants (trees, shrubs, herbs, lianas) dominate in forests. The diversity of plant species is exceptionally high in tropical forests (Adamescu et al. 2018). Walking from the broad daylight in the open savannah into a forest may well feel like a journey from a summer's day into a poorly lit chilled room where the eyes need time to adjust. The ecological elements responsible for the shift from savannah to forest have to do with contour, soil type, humidity, fire frequency, and grazing pressure (Osborne 2000).

In its extreme, trees form a continuous, layered canopy which acts almost as a rooftop. Tree density correlates with annual rainfall, with closed-canopy forests found in the wettest areas. However, even in regions with severe rainfall seasonality, rain forests can persist, as long as the trees have access to water sources (Turner 2001) – although the canopy might not be closed. This is also true for the Gashaka sector, where forests are typically composed of trees with a canopy at 15–35 m height, with some stems rising to more than 40 m.

Trees compete in various ways for access to sunlight, water and nutrients. Complex or deep-reaching underground root growth may provide a competitive edge to access nutrients and water, while growing tall and developing a large crown is a common strategy in the race for light. The latter may explain why many species do not exhibit a linear relation between height and diameter, as growing tall fast goes at the expense of growing thick. Nevertheless, there is a tendency to an asymptote in height, i.e. as the trees grow tall, height growth slows down (Turner 2001), presumably because tree trunks a minimal thickness to avoid breakage. Height is therefore a better predictor of a tree’s individual performance (growth rate, reproductive output, probability of survival) than its age.

Large, thick and mature trees are common in primary old-growth forests. Human activity (grazing, fuelwood collection, burning, logging) often creates secondary forests, which generally contain smaller trees and are also less complex floristically and structurally (Brown 1990).

Vines

Woody climbers – aka vines, lianas or creepers – are plants with flexible climbing stems that rely on other plants (usually trees) for physical support (Pérez-Salicrup & de Meijere 2005). Trees with larger diameters typically carry more climbers (ibid.). They can account for 40 % of a rain forest's species diversity and vegetal biomass (Schnitzer & Bongers 2002). Their fruit, sap and leaves also provide food to forest animals, as well as facilitating the movement of arboreal animals. Although in less quantity, vines also populate temperate forests of the southern and northern hemispheres (Putz & Mooney 1991).

Liana abundance varies with abiotic factors such as rainfall, seasonality and soil fertility (Gentry 1991). Forest disturbances such as trees falling due to age or severe wind or cutting and clearing by humans often favours the growth of woody climbers (Schnitzer & Bongers 2002). However, access to light doesn't seem to be the key factor for the metabolic maintenance of vines, but might be important for their proliferation – which has led some authors to characterize these plants as pioneer species (Gianolli *et al.* 2010).

Vines typically receive little attention in studies of forest ecosystems, not least because of the challenges posed by taxonomic uncertainties (Schnitzer & Bongers 2002) – with the current study not being an exception.

Fruit Production and Dispersal

Plants can proliferate asexually by vegetative reproduction or sexually through the fusion of male and female gametes to form a seed. Flowering plants – angiosperms – are the most common and diverse group of plants. Their procreation relies on pollination, the process by which microscopic grains discharged from the male part of a flower are carried to a receptive female ovule, typically from another plant.

In seed plants, pollen – a fine powdery substance, typically yellow – acts as the mobile vector of genetic material. However, unlike animals, plants cannot actively move to seek out a sexual partner. Thus, to achieve fertilization and germination, they depend on abiotic and biotic factors. Climatic variables such as photoperiod, temperature and precipitation may facilitate pollination via wind or water and the subsequent development of a plant after a period of dormancy. Biotic factors include animals (e.g., insects, birds, bats) that may prey on the flowers, pollinate them or eat fruits, thus expediting seed dispersal (Smith-Ramirez & Armesto 1994).

Rain forest trees are rarely wind-pollinated because their high species diversity provides little chances for a specific male gamete to reach a corresponding female organ. Also, high humidity and rain dampens the pollen and causes its "powder" to stick together, hampering aerial movements. Moreover, the dense canopy filters pollen out and often renders airflow very still, conditions not conducive to wind-assisted pollen transport (Turner 2001).

Generally, plants may flower or fruit during any time. Thus, phenophases may vary greatly, even between closely related forms inhabiting the same forest. This inter- and intraspecific variation in phenophases is particularly expressed in African tropical forests, where flushing, flowering and fruiting can vary from near-perfect intraspecific synchrony to extreme asynchrony, and from perennial activity to repeated short pulses (Adamescu et al. 2018). As a result, flowering of forest trees is notoriously unpredictable.

Nevertheless, there seems to be some association with leaf fall, as leafless trees make flowers more conspicuous and more easily accessible to pollinators. Therefore, in seasonal forests, flowering often coincides with the dry season (Janzen 1967). Once pollinated, flower petals wilt and the seed starts to develop from the ovule. The ovary develops into fruit, which contains the seeds. All other flower parts fall away while ripening, a process influenced by water availability, temperature and humidity (Tutin & Fernandez 1993).

Seeds are then dispersed so as to give rise to a new plant. Seeding may happen simply through fruits falling to the forest floor, whether by gravity or because branches are shaken by sudden rushes of wind or animal movements. If seeds are dispersed by wind, then it is more likely that they ripen during the dry season while air currents are stronger and branches harbour fewer leaves, which enables greater dispersal distances (Chapman et al. 2005).

Seed dispersal may also be facilitated by frugivorous animals attracted to the fleshy expendable parts of fruits. Unripe fruits are normally discretely coloured and generally dry, hard and bitter, ensuring that them becoming attractive for frugivores coincides with seed maturity. Members of frugivorous taxa tend to zoom in on so-called "arillate" seeds that are hairy or fleshy, but more commonly on fruit with brightly coloured, often red or black succulent pulp that resonates against green foliage (Turner 2001). They either manually discard undesirable seeds or ingest them together with the pulp, to then shed these indigestible fruit parts through subsequent defecation (ibid.).

Given the abundance of birds and mammals in tropical forests, it is not surprising that many trees exhibit a "bird-monkey syndrome" (Gautier-Hion 1990). Already early studies recognized the particularly important role primates play as seed dispersers, given that they can access fruit in the canopy itself to consume large quantities, to then spit out or defecate substantial numbers of undamaged seeds (Chapman *et al.* 2017).

The more heavily plants rely on seed-dispersers, the more likely is it that fruit ripens when conditions for dispersal are favourable (Chapman *et al.* 2005). Moreover, the peak of production for animal-dispersed fleshy fruits is likely to coincide with the rainy season, probably because the production of such fruit relies on increased moisture levels (ibid.). If species indeed exhibit a pronounced crop peak – known as "masting" – and if different species are synchronous in their masting, then this is likely to considerably affect the behaviour of plant-eating animals (van Schaik & Pfannes 2005).

Study Aims

The Gashaka long-term data that has been collected on weather and botanical features (see *Ch. 02* and below), adds to the so far few long-term phenology studies of African forests (Adamescu *et al.* 2018). The present research consolidates this considerable bulk of records, with the aim to describe the patterns of climate seasonality. This, in turn, has important consequences on the life-history of plants – and, again in turn, on the socioecology of animals dependent on these, such as primates.

MATERIAL AND METHODS

Climatic Records

Some Nigerian institutions such as universities or government-affiliated are entrusted with collecting weather data. However, such information is hard to come by, because the task is rarely reliably executed. Also, while the GGNP headquarters at Bodel near Serti were fitted with a sophisticated weather station in about 2002, this was never functional.

This research therefore relies on its own weather data, collected at the Gamgam and Kwano study sites. Here, values on rainfall, minimum and maximum temperature as well as humidity were captured via max-min thermometers and hygrometers hung in open but shady space as well as free-standing rain gauges. Records were taken in the evenings at 19:00, and jotted down manually on a daily basis by local field assistants – albeit a few periods were not covered due to malfunction of equipment or sickness. Electronic devices were not employed, as these proved unreliable due to often-extreme weather conditions such as storm, lightning, hail as well as battery failures. Climate data were transcribed into electronic files and mainly compiled by Volker Sommer and the author, GJ.

Botanical Records

Main botanical habitat features were recorded via an 8-km straight *line transect* that consists of two parts of 4 km (Fowler 2006, Pascual-Garrido 2011). These transects were continuously monitored at intervals of two weeks since their establishment in 2002 (*Tab.03.01)*. The transect cuts through the north-western part of Kwano study area (cf. *Fig.02.09*). Transect direction was determined by the intention to incorporate sections of different elevation as well as varying types of habitat, thus allowing a relatively unbiased quantification of the vegetation cover. (No corresponding data exist for the Gamgam study site.)

The aim was to include about 1,000 trees with a diameter at breast height (DBH) of at least 30 cm for the purpose of phenological studies. Trial runs established that for these numbers to work, transect width would have to be 4 m. This method resulted in a final transect sample of 984 trees with 815 associated woody climbers (aka vines, lianas, creepers). Transect trees were permanently labelled, first with strips of local plastic, and since 2006 with professional tree markers out of metal or durable plastic (*www.grube.de*).

Tab.03.01. Phenology records collected along the 8-km straight line transect in the Kwano habitat for trees (n = 984) and associated vines (n = 815), ideally monitored twice per month from Apr02–Dec12. Figures indicate the number of actual monthly data surveys as well as missing records for some periods

Monthly surveys

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2002				2	2	2	2	2	2	2	2	2
2003	2	2	2	2			2	2	2	2	2	1
2004	2	2	2	1								
2005	1	2	2	1	1	2	2	1	1	1	2	2
2006	2	1	2	2	2	2	2	2	2	2	2	2
2007	2	2	2	2	2	2	2	2	2	2	2	2
2008	2	2	2	2	2	2	2	2	2	2	2	2
2009	2	2	2	2	2	2						
2010	2	2	2	2	2	2	2	2	2	2	2	2
2011	2	2	2	2	2	2	2	2	2	2	2	2
2012	2	2	2	2	2	2	2	2	2	2	2	2
Sum	19	19	20	18	15	16	16	15	15	15	16	15

There is no agreement on the correct technical descriptors of closed "forested" or open "savannah" habitats (Osborne 2000). In this study, therefore it was simply distinguished between transect sections that cut through "forest" (more or less closed, including riverine as well as lowland rain forest) and "savannah" (open, sparsely treed savannah-woodland with occasional small patches of treeless grassland).

The height of trees was ascertained via a clinometer or, at times, by comparing a tree with the known height of a neighbouring tree. Most of these measurements were undertaken in about 2003, and refer to 837 trees in which chimpanzees had nested (Fowler 2006). Diameter at breast height (DBH) was recorded for each tree as a standard measure of expressing the girth of a standing trunk. It allows calculations like timber volume or tree growth but also to infer estimates of leaf or fruit production. The number of woody climbers was likewise recorded. DBH and woody climber measurements were undertaken in Mar02 and repeated from Mar–Apr08, by trained local field assistants supervised by various graduate students and researchers.

It should be kept in mind that it is notoriously difficult to "count" vines, as they may cover several trees, and may be entangled with various other climbers. Nevertheless, the aim was to allocate a specific vine to one specific host tree. To achieve this, vines were traced to its roots in the soil and labelled the "first" transect tree the vine climbed on as the "host tree". However, in practice, this was often difficult, as it was difficult to be sure that "the same" vine was monitored throughout successive visits.

In early 2003, an experienced plant taxonomist (Emmanuel Obot, botany professor, Nigeria Conservation Foundation) assigned scientific names to the trees in situ. Of all specimens, 9.4 % remained unidentified, while the remaining 952 trees were identified to either genus (n = 27, 2.8 %) or species level (n = 925, 97.2 %). From Mar–Apr08, a Nigerian PhD student specialised in botany (George Nodza) confirmed that trees of which he had specific taxonomic knowledge had previously been identified correctly. Several unknown species were later identified by senior botanist Benjamin Obajide Daramola of FRIN (Forestry Herbarium Ibadan University) / Nigeria.

Identification of vines has proven difficult and is restricted to a few genera and local names.

Transect trees and vines were monitored within a bracket of three days at the beginning (01st–05th) and in the middle (15th–19th) of each month. Scores were given for the presence resp. absence of fruit, flowers and leaves. The amount of fruit was estimated on an exponential scale (0, 1, 10, 100, 1000, 10000 fruits). Although the distinction between "ripe" and "unripe" fruit is somewhat arbitrary, records were also entered on the quality (ripeness) using size and colour. Data were also collected on fruit remains found at the forest floor as well as the likely identity of arboreal and terrestrial fruit and seed eaters.

The DBH of each tree – measured at 1.2 m from the forest floor during 2002 and 2008 – was taken into account to arrive at estimates of fruit abundance. DBH is a good indicator of both tree size and crown diameter. These are, in turn, good predictors for fruit bearing parts of the vegetation, including biomass and fruit number (Leighton & Leighton 1982). Instead of using estimates from the exponential scale, calculation of fruit productivity was based on the binary of presence / absence of fruit, given that a preliminary analysis had led to very similar results for both methods (Fowler 2006).

Thus, a *fruit index* was calculated for each month by summing up the DBH of all fruit bearing trees on the transect. Because trees with larger DBH can support more vines (Pérez-Salicrup & de Meijere 2005), this approach was extended to woody climbers. Therefore, the *fruit index* of vines was calculated by summing up the DBH of the host trees, assuming that vine fruit production is positively correlated with a host tree's DBH. The DBH of trees and vines were summed up for each month. In previous studies, DBH has been found to be a consistently accurate and precise proxy for fruit production that enables reasonable estimates even for figs and species with large trunks or buttresses (Chapman *et al*. 1992).

For comparison, a much simpler method that relied on the overall percentage of fruiting transect plants was also used.

Phenology data covered in this thesis span 113 months from Apr02–Dec12.The records were entered into electronic data files by GPP-associated PhD students Umaru Buba, Sandra Tranquilli, Alejandra Pascual-Garrido and GJ, amounting to about 180,000 individual data points. Data were analysed by Umaru Buba, Volker Sommer and, for the most part, GJ.

RESULTS

Climate

Long-term records obtained for a 13-yr period (2000–2012) at the Kwano and Gamgam study sites detail and quantify the marked seasonality typical for the north-east of Nigeria in general. Thus, every year, there is a distinct alternation of a single dry season followed by a single rainy season (*Fig.03.02*). The heaviest downpours typically occur from Aug–Sep. Rains tend to cease in Nov and resume sometimes in Apr (*Tab.03.02*). The often-heavy downpours from mid-Apr to mid-Nov constitute 97.2 % of all precipitation. Variables for temperature and humidity mirror this pattern (*Tab.03.03*).

A summative comparison of the Kwano and Gamgam sites is provided in *Tab.03.04*. As for rainfall, Kwano and Gamgam report an average of 41 % resp. 37 % rainy days / month. Yearly average at Kwano is 2,021 mm (range: 1,683–2,337 mm) and the wettest day saw 125 mm rain. In Gamgam, yearly average is 1,916 mm (range: 1,767–2,180 mm) and 152 mm was the maximum registered on a single day. Temperatures at both study sites are similar, with a mean minimum of 21 °C in both places and a mean maximum of 32–33 °C. The hottest day on record saw 42–43 °C. The coolest registered temperature was 14 °C at Kwano and 12 °C at Gamgam.

The seasonal pattern of the environment dramatically effects the plant cover, as illustrated by a tableau of photos depicting the same spot for each month of the year (*Fig.03.03*). Plants grow far more leaves during the rainy season, while leaves wilt and fall off from deciduous trees as and when the dry season progresses. Yearly burning of grass, done deliberately for about 4 months between Dec-Mar, likewise contributes to the dry and brown aspect of scenery during that time.

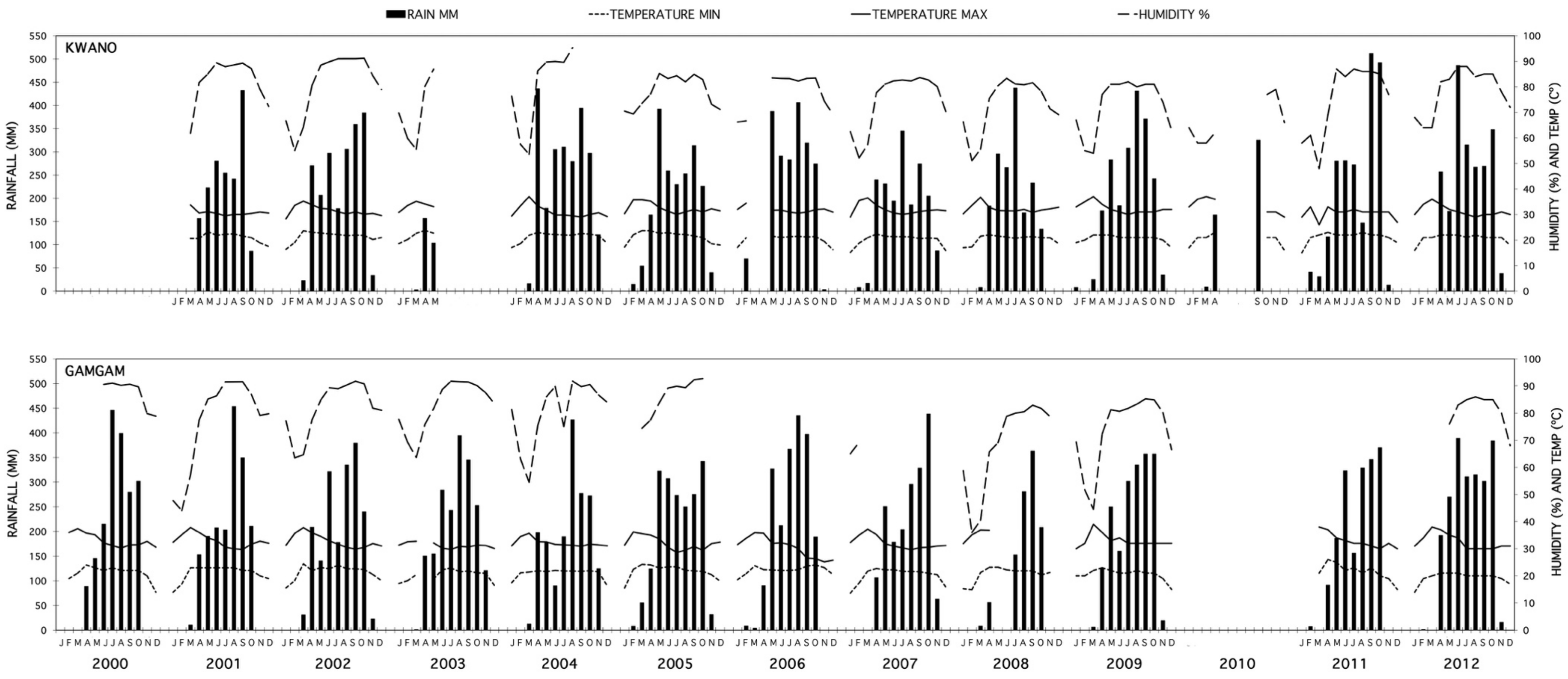

Fig.03.02. Climatic seasonality at Kwano and Gamgam study site (2000–2012). Absent data are indicated by missing characters for those months. Some years in particular have sparse data (Kwano 2000, 2003, 2010; Gamgam 2010)

Tab.03.02. Example of monthly rainfall patterns (years 2011–2012) at Kwano and Gamgam study sites. Figures = mm rain; "x" indicates drizzle

KWANO

DAY	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1							12	8	75	19							20	25	17	1	10	4		
2				X	15	11	20		29	22						25	2	46	14	13	1			
3				X	13	14	10			14						15		18	7	15	20	18	15	
4		1			2	15	3		11							7	17	12			4	11		
5		33				3			15	15	13					3		4		11	9	58		
6					4	32	7		19	7								96		14	12	7		
7					12	6	14		25	19						3	12		14	16	18	4		
8				1	11	11	34	6	21	48						6		12	11	2	8	1	5	
9				2	1	10	8		8	37						19			1		1	15	7	
10						6	5	6	13	8						3	2	12	38	8		12	4	
11						14		19	32	47						7	12		1	1	1	8		
12						8				14						12	15				29	29	5	
13						25	10		7	15						5	24	1	4			3		
14						4	11	1	32	40							3	47	56	15				
15				2	34			1	27	18							4	20	4	3	48			
16				3		2			14	20						24			4	2	12			
17				3	2	12			25	6							2	3		9	7	2		
18				26	12	30	13		2	3						3	7	15	30		1			
19					29		7	7	10	22						19		24	2	1	3	16		
20				3	21		3	23	25	18								30	5	38	8	42		
21			X	X	20	2	3			26				2			7		95	4	6	57		
22		7	31	13	36		11	8	5	31						32	14	8	5	35	1			
23				18	12	8		3	3							45	6	23		1	1	28		
24					20		18	5	17	2						3	7			8	12	8		
25				3	2		8	2	20	5						2		35	3	2	2			
26				X	3		2	25	23	8								8			35	20	2	
27				22	X		4	27	17	15						1	10	22		2	3			
28				21		24	20		20	6						14	3			38	9			
29						8	25		6	7							5	11		5	8			
30					22	36	24	6	11							12	1	14	3	12		5		
31					10														1	11				
Sum	0	41	31	117	280	281	272	147	512	492	13	0	0	2	0	257	172	486	315	267	269	348	38	0

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DAY	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1							17										6	24				24		
2				2	12	18	8	30		10						10	23	15	10					
3					3	5	8		20	27								13	28	8	10	5		
4					3	13	2		22	4							1	56	8		5	40		
5						20				36							34			13	15			
6						32		1		16								26		10	29	18		
7					7	3				2							9		6	20	8	6		
8					9	2	1	10	18	35								3			22		5	
9						14	4		5	18						10			41			21	4	
10						7	4		2	15						2	3	4	10			13	7	
11					32			14	20	3							12					11		
12						60	5			8							3				16	8		
13					20	3	4		12	6							4	30	24			18		
14					8	13	1	3	33	2								22	26	23,0				
15									40	26							2	23		12	33			
16				2					9	10							17	9			3	10		
17				3	7	20			20							4			8	9		13		
18				4	5	5		18	3	14						5	21			5	33			
19				10			18	36	3	12							13	12	10			60		
20				2	5		8		45	18							46	32		28	13			
21				22			13		29	16							5	6		5	18	10		
22						84		20	2	55				1			10		87					
23		7		2	15	3		8	2							28	6			12		71		
24					2				4	20						10		4		10	20	10		
25					7		3		12							43	13	7		6				
26								78	2							13		10		30	46	15		
27				18				6	5								10	43			13			
28				3	17	18	48	15	18							17	18	11		73				
29						3	10		20	13										17		7		
30				23	18			36		4						18		4	48	20	18	24		
31					16		2	54									20	35	5	14				
Sum	0	7	0	91	186	323	156	329	346	370	0	0	0	1	0	160	276	389	311	315	302	384	16	0

Tab.03.03. Summary of weather parameters at Kwano and Gamgam study sites (2000–2012). Humidity measured at 18:00–19:00, except for Gamgam 2000–2007, when values for 08:00 were used. Value for total rainfall at Kwano was adjusted in 2 individual years (indicated by asterisks) by adding averages from other years to compensate for months without data (2001: Mar; 2006: Mar, Apr). (Modified, extended and corrected after Sommer & Ross 2011b)

KWANO

Coolest day (° C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MIN
2001	-	-	18	17	17	21	21	20	20	18	16	16	16
2002	14	16	22	20	21	20	21	20	20	20	17	15	14
2003	14	17	20	22	21	-	-	-	-	-	-	-	14
2004	16	16	20	21	21	20	21	21	20	21	19	16	16
2005	14	19	22	22	21	21	20	20	20	20	16	16	14
2006	17	19	-	-	20	20	20	21	19	20	15	14	14
2007	14	16	18	21	21	18	20	20	20	20	17	14	14
2008	14	16	20	21	20	20	20	20	19	20	17	15	14
2009	15	16	20	21	21	20	20	20	20	20	17	15	15
2010	15	18	19	21	-	-	-	20	-	20	19	15	15
2011	14	17	19	21	20	20	20	21	21	20	19	15	14
2012	14	18	19	19	20	19	20	20	20	20	18	15	14
MIN	14	16	18	17	17	18	20	20	19	18	15	14	14

Hottest day (°C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MAX
2001	-	-	43	35	35	34	32	34	33	33	32	35	43
2002	31	39	37	39	34	36	36	34	35	34	32	32	39
2003	35	37	38	38	36	-	-	-	-	-	-	-	38
2004	31	36	40	37	35	33	31	34	32	32	33	31	40
2005	31	36	40	37	35	33	31	34	32	32	33	31	40
2006	36	40	39	39	35	34	33	34	34	33	35	34	40
2007	35	37	-	-	36	35	33	32	33	33	33	33	37
2008	29	38	41	37	34	33	32	32	33	35	34	33	41
2009	35	39	39	37	33	33	32	35	33	35	33	35	39
2010	36	40	41	38	-	-	-	-	-	32	32	31	41
2011	33	35	38	39	34	35	35	34	33	33	33	30	39
2012	33	36	38	37	34	33	32	31	32	33	33	32	38
MAX	36	40	43	39	36	36	36	35	35	35	35	35	43

Mean max. temp. (°C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MEAN
2001	-	-	34	31	31	30	30	30	30	30	31	31	31
2002	28	34	35	34	32	32	31	30	31	30	30	30	31
2003	31	34	35	34	33	-	-	-	-	-	-	-	33
2004	29	33	37	33	32	30	30	30	29	30	31	29	31
2005	30	36	36	35	33	31	30	31	32	31	32	31	32
2006	32	34	-	-	32	32	31	31	31	32	32	31	32
2007	29	35	37	34	32	31	30	30	31	32	32	32	32
2008	30	34	37	33	32	31	31	32	31	32	32	33	32
2009	33	35	37	34	32	31	30	31	31	31	32	32	32
2010	33	36	37	36	-	-	-	31	-	31	31	29	33
2011	29	33	26	33	31	31	32	31	31	31	31	27	31
2012	30	34	36	34	32	31	30	29	30	30	31	30	31
MEAN	30	34	35	34	32	31	30	31	31	31	31	30	32

Mean min. temp. (°C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MEAN
2001	-	-	21	21	23	22	22	22	22	21	19	18	21
2002	16	19	24	23	23	22	22	22	22	22	20	21	21
2003	19	20	23	24	23	-	-	-	-	-	-	-	22
2004	17	19	22	23	22	22	22	22	23	22	22	19	21
2005	17	22	24	24	23	23	22	22	22	21	19	18	21
2006	17	21	-	-	22	21	21	21	21	21	19	16	20
2007	15	19	21	22	22	21	21	21	21	21	21	16	20
2008	17	17	22	22	22	21	21	21	21	21	21	19	20
2009	19	20	22	22	22	21	21	21	21	21	20	17	21
2010	17	21	21	23	-	-	-	21	-	21	21	16	20
2011	15	21	22	23	22	22	22	23	22	22	21	19	21
2012	16	21	21	22	22	22	21	22	21	21	21	18	21
MEAN	17	20	22	23	22	22	22	22	21	21	20	18	21

Mean humidity (%)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MEAN
2001	.	.	62	82	85	89	88	89	89	87	79	72	82
2002	67	55	64	81	88	90	91	91	91	91	84	79	81
2003	70	60	56	80	87	-	-	-	-	-	-	-	70
2004	76	58	54	86	90	90	90	95	-	-	-	-	80
2005	70	69	74	77	85	83	84	82	85	83	73	71	78
2006	66	67	-	-	84	83	83	82	83	83	74	69	-
2007	62	54	57	78	81	82	83	82	84	83	80	70	-
2008	66	51	56	75	80	83	81	81	82	78	71	69	73
2009	67	55	54	77	81	81	82	80	81	81	74	63	73
2010	64	58	58	62	-	-	86	-	-	77	79	66	69
2011	58	61	48	69	87	84	87	86	86	85	77	-	75
2012	68	64	64	82	83	88	88	84	85	85	78	72	78
MEAN	67	59	59	77	85	85	86	85	85	83	77	70	76

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Coolest day (° C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MIN
2000	-	17	16	21	22	21	21	20	21	21	16	16	16
2001	13	14	19	20	20	22	21	20	21	19	17	13	13
2002	13	14	19	16	21	20	21	21	21	21	17	14	13
2003	13	13	17	-	16	19	19	19	20	19	18	13	13
2004	15	19	19	19	16	20	21	20	20	21	16	14	14
2005	14	19	22	22	21	22	20	19	21	20	17	16	14
2006	16	16	22	18	21	21	21	21	22	22	18	17	16
2007	12	12	18	18	21	20	20	21	20	20	17	13	12
2008	13	13	18	20	21	21	21	21	21	18	20	-	13
2009	15	15	16	21	21	20	20	20	20	20	16	14	14
2010	-	-	-	-	-	-	-	-	-	-	-	-	-
2011	-	-	20	21	21	22	21	21	21	20	17	13	13
2012	15	17	20	20	20	20	19	21	20	20	17	15	15
MIN	12	12	16	16	16	19	19	19	20	18	16	13	12

Hottest day (°C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MAX
2000	-	39	41	40	38	35	35	33	34	33	34	32	41
2001	35	39	40	39	37	36	35	34	33	34	34	34	40
2002	34	39	39	42	36	36	35	33	33	33	36	34	42
2003	34	39	36	-	34	36	36	36	33	33	32	32	39
2004	33	42	41	37	36	34	33	33	34	33	34	33	42
2005	36	40	39	40	38	35	36	34	33	33	35	34	40
2006	34	38	38	40	34	34	34	33	34	28	28	28	40
2007	37	38	40	39	36	35	33	32	32	32	32	34	40
2008	34	39	41	42	-	35	34	34	34	37	33	-	42
2009	38	37	41	40	36	38	35	36	33	34	33	34	41
2010	-	-	-	-	-	-	-	-	-	-	-	-	-
2011	-	-	41	39	38	36	36	35	34	33	33	32	41
2012	33	37	39	39	39	41	33	32	33	32	32	31	41
MAX	38	42	41	42	39	41	36	36	34	37	36	34	42

Mean max. temp. (°C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MEAN
2000	-	36	37	36	35	32	31	30	31	31	33	31	33
2001	32	35	38	36	34	33	31	30	30	32	33	32	33
2002	31	36	38	36	35	33	32	30	30	30	32	31	33
2003	31	33	33	-	32	30	30	31	31	31	31	30	31
2004	31	35	36	33	33	32	31	31	31	32	31	31	32
2005	31	36	36	35	34	31	29	29	31	29	32	32	32
2006	32	34	36	36	32	32	32	30	27	26	25	26	31
2007	32	35	37	35	32	31	30	30	30	31	31	31	32
2008	32	35	37	37	-	-	-	-	-	-	-	-	35
2009	30	32	39	36	33	34	32	32	32	32	32	32	33
2010	-	-	-	-	-	-	-	-	-	-	-	-	-
2011	-	-	38	37	34	33	32	32	31	30	32	30	33
2012	31	34	38	37	35	34	30	30	30	30	31	31	33
MEAN	31	35	37	36	33	32	31	31	30	30	31	31	33

Mean min. temp. (°C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MEAN
2000	-	19	21	24	23	22	23	22	22	22	20	14	21
2001	14	17	23	23	23	23	23	23	22	22	20	19	21
2002	16	18	24	22	23	23	24	23	23	22	21	18	21
2003	17	18	20	-	19	22	23	21	22	21	21	16	20
2004	18	21	21	22	22	22	22	22	22	22	22	16	21
2005	16	22	24	24	23	23	23	22	22	22	20	18	22
2006	19	21	24	22	22	22	22	22	24	24	23	20	22
2007	14	17	22	23	22	22	22	22	22	21	20	16	20
2008	15	15	21	23	23	22	22	22	22	20	21	-	21
2009	20	20	22	23	22	21	21	22	21	21	19	15	21
2010	-	-	-	-	-	-	-	-	-	-	-	-	-
2011	-	-	21	26	25	22	23	21	23	20	19	15	22
2012	14	19	20	21	21	21	20	20	20	20	19	17	19
MEAN	16	19	22	23	22	22	22	22	22	21	20	17	21

Mean humidity (%)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MEAN
2000	-	-	-	-	-	91	91	90	91	90	80	79	87
2001	48	44	57	78	85	86	92	92	92	87	79	80	77
2002	77	64	65	78	85	89	89	90	92	91	82	81	82
2003	78	69	64	76	82	89	92	92	91	90	88	84	83
2004	81	63	55	75	86	90	75	92	90	91	87	84	81
2005	80	-	74	78	84	89	90	89	92	93	-	-	85
2006	-	-	-	-	-	-	-	-	-	-	-	-	-
2007	65	69	-	-	-	-	-	-	-	-	-	-	-
2008	59	36	41	66	69	79	80	81	83	82	79	-	68
2009	69	52	45	72	81	81	82	83	85	85	80	67	74
2010	-	-	-	-	-	-	-	-	-	-	-	-	-
2011	-	-	-	-	-	-	-	-	-	-	-	-	-
2012	-	-	-	-	76	83	85	86	85	85	80	68	81
MEAN	70	57	57	75	81	86	86	88	89	88	82	77	80

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Rain days / month (%)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MEAN
2001	0	0	0	53	68	73	74	68	73	45	0	0	38
2002	0	0	10	50	61	63	55	84	57	74	10	0	39
2003	0	0	6	47	42	-	-	-	-	-	-	-	19
2004	0	0	13	63	77	60	52	58	70	48	33	0	40
2005	0	11	29	40	84	77	58	61	87	71	7	0	44
2006	0	21	-	-	87	87	68	74	87	84	7	0	51
2007	0	4	13	60	68	60	68	68	70	55	23	0	41
2008	0	0	3	60	77	63	71	68	53	26	0	0	35
2009	0	0	7	70	96	69	90	93	91	81	20	0	52
2010	0	0	7	48	50	-	-	92	83	-	0	0	31
2011	0	11	3	44	74	72	74	52	90	87	4	0	43
2012	0	4	0	78	80	76	65	81	87	65	21	0	46
MEAN	0	4	8	56	72	70	67	73	77	64	11	0	40

Wettest day (mm rain)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MAX
2001	0	0	0	51	45	45	32	65	122	23	0	0	122
2002	0	0	15	70	48	41	55	50	65	49	14	0	70
2003	0	0	2	65	21	-	-	-	-	-	-	-	65
2004	0	0	7	70	30	104	63	93	63	90	22	0	104
2005	0	11	14	44	59	45	39	41	40	30	26	0	59
2006	0	37	-	-	47	41	34	82	91	35	3	0	91
2007	0	8	9	40	61	26	82	67	68	40	27	0	82
2008	0	0	8	47	37	51	125	25	64	76	0	0	125
2009	8	0	13	27	40	32	35	69	122	58	9	0	122
2010	0	0	5	31	-	-	-	-	55	-	0	0	55
2011	0	33	31	26	36	36	34	27	75	48	13	-	75
2012	0	2	0	45	24	96	95	38	48	58	15	0	96
MAX	8	37	31	70	61	104	125	93	122	90	27	0	125

Rain (mm)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	TOTAL
2001	0	0	-	157	222	280	255	242	432	86	0	0	1683 *
2002	0	0	23	270	207	297	178	306	359	384	34	0	2056
2003	0	0	3	157	104	-	-	-	-	-	-	-	-
2004	0	0	16	436	179	305	310	279	394	297	122	0	2337
2005	0	15	54	164	392	259	230	253	314	226	40	0	1945
2006	0	70	-	-	387	291	283	406	319	274	3	0	2279 *
2007	0	8	17	240	231	194	345	186	274	205	87	0	1786
2008	0	0	8	184	296	266	437	169	233	134	0	0	1726
2009	8	0	25	173	283	184	308	431	371	242	35	0	2060
2010	0	0	9	164	-	-	-	-	325	-	0	0	-
2011	0	41	31	117	280	281	272	147	512	492	13	-	2186
2012	0	0	0	257	172	486	315	267	269	348	38	0	2152
MEAN	1	11	18	211	250	284	293	268	346	269	34	0	2021

Temp. Fluctuation (°C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MAX
2001	12	15	12	11	10	10	9	9	9	8	10	9	15
2002	12	13	13	10	10	-	-	-	-	-	-	-	13
2003	12	15	15	10	9	8	8	8	6	8	9	11	15
2004	13	14	12	12	10	8	8	9	10	10	14	13	14
2005	15	14	-	-	10	11	10	9	10	11	13	15	15
2006	14	17	16	11	10	9	9	9	11	11	11	16	17
2007	13	16	15	11	10	10	11	11	10	11	11	14	16
2008	14	15	15	12	10	10	9	10	10	10	12	15	15
2009	16	15	16	13	-	-	-	10	-	10	10	13	16
2010	14	12	4	10	9	9	10	8	9	9	10	8	-
2011	14	13	15	12	10	9	9	7	9	9	10	12	15
2012	14	14	13	11	10	9	9	9	9	10	11	13	14
MAX	16	17	16	13	10	11	11	11	11	11	14	16	17

Average Temp (°C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MEAN
2001	-	-	27	26	27	26	26	26	26	26	25	24	26
2002	22	26	29	28	28	27	27	26	26	26	25	25	26
2003	25	27	29	-	28	-	-	-	-	-	-	-	27
2004	23	26	29	28	27	26	26	26	26	26	26	24	26
2005	24	29	30	29	28	27	26	27	27	26	25	25	27
2006	25	28	-	-	27	26	26	26	26	27	26	24	26
2007	22	27	29	28	27	26	26	26	26	26	26	24	26
2008	24	25	29	27	-	-	-	-	-	-	-	-	26
2009	26	28	30	28	27	26	26	26	26	26	26	25	27
2010	-	-	-	-	-	-	-	-	-	-	-	-	-
2011	-	-	24	28	27	27	27	27	27	27	26	23	26
2012	23	28	29	28	27	27	26	26	26	26	26	24	26
MEAN	24	27	28	28	27	26	26	26	26	26	26	24	26

GAMGAM

Rain days / month (%)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MEAN
2000	0	0	0	57	48	63	58	71	60	58	0	0	35
2001	0	0	6	40	58	57	71	55	70	52	0	0	34
2002	0	0	6	43	52	67	58	65	67	58	7	0	35
2003	0	0	3	33	35	73	58	68	80	77	23	0	38
2004	0	0	3	50	65	30	65	58	57	52	30	0	34
2005	0	7	6	30	55	67	65	52	73	65	7	0	35
2006	0	4	6	13	55	63	61	55	70	65	-	-	39
2007	-	-	-	47	52	53	55	55	73	71	16	0	47
2008	0	0	3	27	-	-	78	55	72	29	-	-	33
2009	0	0	7	52	65	70	74	77	89	71	18	0	44
2010	-	-	-	-	-	-	-	-	-	-	-	-	-
2011	0	4	0	37	57	62	55	45	77	74	0	0	34
2012	0	3	0	46	68	70	42	58	53	61	10	0	34
MEAN	0	2	4	38	56	61	62	58	71	61	12	0	37

Wettest day (mm rain)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MAX
2000	-	0	0	21	26	69	99	57	53	78	0	0	99
2001	0	0	9	31	32	38	64	144	53	53	0	0	144
2002	0	0	22	32	23	43	29	54	58	36	18	0	58
2003	0	0	1	43	62	36	39	89	75	46	56	0	89
2004	0	0	12	41	30	29	31	152	34	70	54	0	152
2005	0	6	41	42	103	40	39	52	50	53	23	0	103
2006	0	8	3	36	95	47	74	83	114	40	-	-	114
2007	-	-	-	34	50	26	33	61	51	55	23	0	61
2008	0	0	8	13	-	-	75	45	60	31	-	-	75
2009	0	0	5	23	35	25	41	41	70	106	7	0	106
2010	-	-	-	-	-	-	-	-	-	-	-	-	-
2011	-	7	-	23	32	84	48	78	45	55	0	0	84
2012	0	1	0	43	46	56	87	73	46	71	7	0	87
MAX	0	8	41	43	103	84	99	152	114	106	56	0	152

Rain (mm)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	TOTAL
2000	-	0	0	89	145	215	446	399	280	302	0	0	1875
2001	0	0	10	153	190	207	203	453	349	211	0	0	1777
2002	0	0	31	209	140	321	178	335	379	240	23	0	1856
2003	0	0	1	150	155	284	243	395	345	253	121	0	1946
2004	0	0	12	198	178	90	190	426	277	272	125	0	1767
2005	0	8	55	124	323	307	273	250	275	342	31	0	1989
2006	0	8	4	90	327	212	367	435	397	189	-	-	2081
2007	-	-	-	106	251	178	204	296	329	438	63	0	1882
2008	0	0	8	56	-	-	153	281	363	208	-	-	-
2009	0	0	6	126	250	160	302	335	357	357	19	0	1912
2010	-	-	-	-	-	-	-	-	-	-	-	-	-
2011	-	7	-	91	186	323	156	329	346	370	0	0	1808
2012	0	1	0	192	270	389	311	315	302	384	16	0	2180
MEAN	0	2	13	132	219	244	252	354	333	297	40	0	1916

Temp. Fluctuation(°C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MAX
2000	-	17	16	12	12	10	8	8	9	9	13	17	17
2001	18	18	15	13	11	10	8	7	8	10	13	13	18
2002	16	17	13	14	11	10	8	8	7	8	11	13	17
2003	14	14	12		13	8	7	9	9	10	10	14	14
2004	14	13	14	11	11	10	10	10	9	10	10	15	15
2005	16	14	11	11	11	7	5	7	9	8	11	14	16
2006	13	13	12	13	10	10	10	8	3	2	2	5	13
2007	19	18	15	13	10	9	9	8	9	10	11	15	19
2008	17	20	16	14	-	-	-	-	-	-	-	-	20
2009	10	12	17	13	11	13	11	10	11	11	13	17	17
2010	-	-	-	-	-	-	-	-	-	-	-	-	-
2011	-	-	17	11	9	11	9	11	8	10	13	15	17
2012	17	15	18	16	14	13	10	10	10	10	12	14	18
MAX	19	20	18	16	14	13	11	11	11	11	13	17	20

Average Temp (°C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	MEAN
2000	-	28	29	30	29	27	27	26	27	27	26	22	27
2001	23	26	30	30	29	28	27	26	26	27	26	26	27
2002	23	27	31	29	29	28	28	27	26	26	26	25	27
2003	24	25	27	-	25	26	26	26	26	26	26	23	26
2004	24	28	29	27	27	27	27	27	26	27	26	24	27
2005	23	29	30	30	28	27	26	26	26	26	26	25	27
2006	25	27	30	29	27	27	27	26	25	25	24	23	26
2007	23	26	29	29	27	27	26	26	26	26	26	24	26
2008	24	25	29	30	-	-	-	-	-	-	-	-	27
2009	25	26	31	30	28	28	27	27	27	27	26	24	27
2010	-	-	-	-	-	-	-	-	-	-	-	-	-
2011	-	-	30	32	30	28	28	27	27	25	26	23	27
2012	23	27	29	29	28	28	25	25	25	25	25	24	26
MEAN	24	27	29	29	28	27	27	26	26	26	26	24	27

Tab.03.04. Main climatic variables at Kwano and Gamgam study sites: Similarities and differences

Variable (2000–2012)	Kwano	Gamgam	Difference
Maximum temperature (ºC)			
Average across years	31.9	32.5	-0.7
Minimum monthly mean	26.0	25.2	0.8
Maximum monthly mean	37.0	39.0	-2.0
Highest daily value	43.0	42.0	1.0
Lowest daily value	29.0	28.0	1.0
Minimum temperature (ºC)			
Average across years	20.8	20.9	-0.1
Minimum monthly mean	15.0	13.6	1.4
Maximum monthly mean	23.8	26.0	-2.2
Highest daily value	22.0	22.0	0.0
Lowest daily value	13.5	11.5	2.0
Average temperature (^{o}C)			
Mean of average minimum and maximum	26.3	26.7	-0.4
Humidity %)			
Average across years	76.2	79.7	-3.5
Minimum monthly mean	48.0	36.0	12.0
Maximum monthly mean	98.5	93.0	5.5
Rain (mm)			
Average across years	2021.0	1915.7	105.3
Minimum monthly mean	0.0	0.0	0.0
Maximum monthly mean	512.0	453.4	58.6
Highest daily value	125.0	152.0	-27.0
Lowest daily value	0.0	0.0	0.0
Rainy days / month (%)	40.9	36.7	4.2

JANUARY FEBRUARY MARCH

APRIL MAY JUNE

JULY AUGUST SEPTEMBER

OCTOBER NOVEMBER DECEMBER

Fig.03.03. Seasonal change in vegetation cover over the course of a year. Standardised view from Kwano research station towards surrounding savannah, with forest and hills in background (Jan–Dec12). Plant productivity peaks during the height of the rainy season from May–Oct. Grass burning is common during the dry season, in this case in Feb. (Photos: GJ and Maigari Ahmadu on instruction by GJ)

Tab.03.05. Trees growing along 8 km of straight-line transect at Kwano (established 2002; 4 m wide; with 984 trees and 815 associated vines). The species of 901 trees could be identified by Prof Emmanuel Obot (NCF); names of common species independently verified by botany student George Nodza. Fulani and Hausa names independently provided by local field assistants Bobbo Buba and Hammaunde Guruza. English vernacular names researched by Alejandra Pascual-Garrido. (Corrected, modified and extended after Fowler 2006: Tab.2.7)

Family	Name	English name	Fulani	Hausa	Specimens on transect (n)	Specimens on transect (%)	Source (a)
Fabaceae	*Afzelia africana*	Mahogany bean, African mahogany		Kawo	1	0,1	
Mimosoideae	*Albizia intermedia*				2	0,2	
Mimosoideae	*Albizia zygia*				4	0,4	
Euphorbiaceae	*Alchornea cordifolia*	Christmas bush			1	0,1	
Sapotacea	*Aningeria altissima*				1	0,1	(1)
Annonaceae	*Annona senegalensis*	wild custard apple		Gwandan daji	6	0,7	(6)
Combretaceae	*Anogeissus leiocarpus*	axlewood	Kojoli	Marke	61	6,8	
Caesalpinoideae	*Anthonota crassifolia*				5	0,6	
Caesalpinoideae	*Anthonota lamprophyllum*				3	0,3	
Euphorbiaceae	*Anthostema aubryanum*				1	0,1	(6)
Moraceae	*Antiaris toxicaria*	ark cloth tree, antiaris, false iroko, false mvule, upas tree			1	0,1	(6)
Rutaceae	*Araliopsis tabouensis*				1	0,1	
Fabaceae	*Berlinia bracteosa*				1	0,1	(6)
Melianthaceae	*Bersama abyssinica*	winged bersama		Loko	1	0,1	(6)
Sapindaceae	*Blighia sapida*	akee apple			12	1,3	(6)
Bombaceae	*Bombax costatum*	red-flowered silk cotton tree			3	0,3	
Caesalpinoideae	*Brachystegia eurycoma*		Wambo		15	1,7	
Euphorbiaceae	*Bridelia*				3	0,3	
Euphorbiaceae	*Bridelia atroviridis*	rare forest bridelia			19	2,1	
Euphorbiaceae	*Bridelia ferruginea*		Mbori	Dargaza	28	3,1	
Euphorbiaceae	*Bridelia lutea*		Burumburum		9	1,0	
Euphorbiaceae	*Bridelia macrantha*	bridelia, coast goldleaf	Burumburum		7	0,8	(3)
Euphorbiaceae	*Bridelia speciosa*		Burumburum		19	2,1	
Fabaceae	*Burkea africana*	wild seringa		Karya gatari	1	0,1	
Burseraceae	*Canarium schweinfurthii*	African elemi		Atile	1	0,1	
Bombacaceae	*Ceiba pentandra*	silk cotton tree, Kapok	Bantahi	Rimi	2	0,2	
Ulmaceae	*Celtis*				2	0,2	
Ulmaceae	*Celtis africana*	white stinkwood			1	0,1	
Ulmaceae	*Celtis zenkeri*				1	0,1	
Sapotacea	*Chrysophyllum subnudum*	Adasema			3	0,3	(1)
Verbenaceae	*Clerodendrum thomsoniae*	bleeding glory-bower glory-bower, bagflower, bleeding-heart vine			1	0,1	(6)
Rubiaceae	*Coffea canephoria*				6	0,7	
Sterculiaceae	*Cola gigantea*	giant cola	Kukahi		30	3,4	(1)
Sterculiaceae	*Cola hispida*				4	0,4	(1)
Sterculiaceae	*Cola millenii*	monkey kola			11	1,2	
Combretaceae	*Combretum molle*	velvet bush willow, velvet leaf combretum, velvet leaf willow			1	0,1	(3)centre
Capparidaceae	*Crateva adansonii*	garlic pear tree, three-leaf caper, obtuse leaf crateva			1	0,1	
Rubiaceae	*Crossopteryx febrifuga*	African bark	Rima joga	Kashin awaki	49	5,5	(1)
Araliaceae	*Cussonia arborea*	octopus cabbage tree	Jumbali		14	1,6	(4)
Caesalpinoideae	*Daniellia oliveri*	West African copal, African copaiba balsam tree	Karlahi	Magie, Maje	7	0,8	(5)
Caesalpinoideae	*Dialium guineense*	black velvet, velvet tamarind	Kom	Samiyan biri	6	0,7	(3)
Fabaceae	*Dichrostachys cinerea*	sickle bush	Burlehi		1	0,1	(2)
Ebenaceae	*Diospyros*		Balehi nyamnyam		2	0,2	
Ebenaceae	*Diospyros mespiliformis*	West African ebony, African ebony, jackal-berry	Balehi nyamnyam		2	0,2	(2)
Malvaceae	*Dombeya buettneri*				3	0,3	
Dracaenaceae	*Dracaena arborea*	tree dracaena	Lera		1	0,1	(1)
Putranjivaceae	*Drypetes*				2	0,2	(6)
Meliaceae	*Ekebergia senegalensis*		Red Karehi		11	1,2	(1)
Palmae	*Elaeis guineensis*	oil palm		Kwara	4	0,4	(6)
Clusiaceae	*Endodesmia pentadesma*				1	0,1	

Family	Name	English name	Fulani	Hausa	Specimens on transect (n)	Specimens on transect (%)	Source (a)
Meliaceae	*Entandrophargma candollei*				1	0,1	(6)
Meliaceae	*Entandrophragma utile*	African cedar, Ashanti cedar, budongo heavy mahogany, feather sepele, mahogany, mufumbi mahogany, sipo mahogany			1	0,1	(3)
Papilionoideae	*Erythrina sigmoidea*				4	0,4	(1)
Caesalpinoideae	*Erythrophleum suaveolens*	sasswood, poison wood tree		Gwaska	13	1,5	(1)
Erythroxylaceae	*Erythroxylum emarginatum*	African coca tree, common coca tree		Gwaska	4	0,4	(4)
Moraceae	*Ficus exasperata*	sandpaper tree			1	0,1	(1)
Moraceae	*Ficus lutea*	giant-leafed fig	Durumihi	Farin gamji	12	1,3	(2)
Moraceae	*Ficus mucoso*				1	0,1	
Moraceae	*Ficus ovata*	fig tree			1	0,1	(1)
Moraceae	*Ficus sur*	bush fig	Ibbal	Baure	5	0,6	
Moraceae	*Ficus trichopoda*	swamp fig			1	0,1	
Moraceae	*Ficus vallis-choude*	fig tree	Ibbal danejum, Rima bechi	Baure, Farin baure	9	1,0	
Moraceae	*Ficus vogeliana*				1	0,1	
Guttiferae	*Garcinia afzelii*	bitter kola	Bura lainde		2	0,2	
Guttiferae	*Garcinia smeathmannii*				2	0,2	
Clusiaceae	*Harongana madagascarensis*				1	0,1	(6)
Annonaceae	*Hexalobus monopetalus var. parvifolius*			Gondan kurmi	7	0,8	(1)
Salicaceae	*Homalium dalzielii*		Mahbelko lainde		6	0,7	(6)
Euphorbiaceae	*Hymenocardia acida*		Ngaluwaje, Samataje	Janyaro	19	2,1	(1)
Meliaceae	*Khaya senegalensis*	African mahogany	Dalehi	Madachi, Mahoga	16	1,8	
Bignoniaceae	*Kigelia africana*	sausage tree			2	0,2	
Anacardiaceae	*Lannea*				3	0,3	
Anacardiaceae	*Lannea acida*		Muratuta		19	2,1	(1)
Anacardiaceae	*Lannea avvic*				1	0,1	
Anacardiaceae	*Lannea barteri*				1	0,1	(1)
Anacardiaceae	*Lannea kerstingii*				3	0,3	(1)
Anacardiaceae	*Lannea nigritana*	wodier wood			2	0,2	
Ochnaceae	*Lophira lanceolata*	red iron wood	Sakto, Pirohi	Jatau, Namijin kadanya	2	0,2	
Meliaceae	*Lovoa trichilioides*	african walnut			1	0,1	(6)
Euphorbiaceae	*Macaranga*		Dalamhi		3	0,3	
Euphorbiaceae	*Macaranga barteri*				2	0,2	(1)
Euphorbiaceae	*Macaranga schweinfurthii*		Dalamhi		10	1,1	(1)
Maesaceae	*Maesa lanceolata*	false assegai			1	0,1	(2)
Sapotaceae	*Malacantha alnifola*				16	1,8	
Bignoniaceae	*Markhamia lutea*	Nile tulip tree			1	0,1	(5)
Bignoniaceae	*Markhamia tomentosa*				5	0,6	(1)
Celastraceae	*Maytenus senegalensis*	confetti tree	Yayehi		1	0,1	
Annonaceae	*Monodora myristica*	Calabash nutmeg			1	0,1	
Chrysobalanaceae	*Parinari curatellifolia*		Nawarre baadi	Fara rura	1	0,1	
Dipterocarpaceae	*Monotes kerstingii*		Naude	Tuwon biri	3	0,3	
Dipterocarpaceae	*Monotes polyandra*		Naude	Tuwon biri	1	0,1	
Rubiaceae	*Morelia senegalensis*				1	0,1	
Lecythidaceae	*Napoleonaea talboti*				1	0,1	
Rubiaceae	*Nauclea latifolia*	African peach, pin cushion tree	Bakurahi	Tafasia	5	0,6	
Ochnacea	*Ochna membranacea*				1	0,1	(1)
Ochnacea	*Ochna schweinfurthiana*	brick-red ochna			15	1,7	(1)
Pandanaceae	*Pandanus candelabrum*	screw pine	Butol tigon	Ananan daji	2	0,2	(1)

Family	Name	English name	Fulani	Hausa	Specimens on transect (n)	Specimens on transect (%)	Source (a)
Mimosoideae	*Parkia*		Wang		3	0,3	
Mimosoideae	*Parkia bicolor*	bicolor parkia	Wang	Dorowa	9	1,0	
Mimosoideae	*Parkia biglobosa*	locust bean tree	Nareje		6	0,7	
Arecaceae	*Phoenix reclinata*	wild date palm	Bali darle		1	0,1	(2)
Caesalpinoideae	*Piliostigma thonningii*	camel foot	Barkehi	Kargo	23	2,6	
Mimosoideae	*Piptadeniastrum africanum*				2	0,2	(1)
Araliaceae	*Polyscias fulva*	parasol tree			1	0,1	(4)
Meliaceae	*Pseudocedrela kotschyi*	dry zone cedar	Wada wurohi		1	0,1	(1)
Anacardiaceae	*Pseudospondias microcarpa*	African grape	Mugum		19	2,1	(1)
Guttiferae	*Psorospermum febrifugum*	christmas berry	Sawalki		1	0,1	(4)
Fabaceae	*Pterocarpus erinaceus*	African rosewood	Iyamhi	Madubiya	6	0,7	
Myristicaceae	*Pycnanthus angolensis*	African nutmeg			2	0,2	
Myristicaceae	*Pycnanthus euronasius [?]*		Iyamhi	Madubiya	1	0,1	
Rubiaceae	*Rothmannia hispida*				1	0,1	(6)
Bignoniaceae	*Spathodea*				2	0,2	
Bignoniaceae	*Spathodea campanulata*	African tuliptree			4	0,4	(6)
Euphorbiaceae	*Spondianthus preussii*				1	0,1	(6)
Malvaceae	*Sterculia*				3	0,3	
Malvaceae	*Sterculia oblonga*	yellow sterculia	Bodahi		29	3,2	(6)
Malvaceae	*Sterculia rhinopetala*				2	0,2	
Malvaceae	*Sterculia tragacantha*	African tragacanth			2	0,2	(1)
Bignoniaceae	*Stereospermum*				2	0,2	
Bignoniaceae	*Stereospermum kunthianum*	pink jacaranda	Golombe		3	0,3	
Olacaceae	*Strombosia pustulata*		Ciwo lainde		7	0,8	(1)
Clusiaceae	*Symphonia globulifera*		Chabbole lainderi		1	0,1	
Sapotaceae	*Synsepalum*		Karehi	Kadanya	1	0,1	
Sapotaceae	*Synsepalum dulcificum*	miracle fruit			4	0,4	(6)
Sapotaceae	*Synsepalum glycydorum*				1	0,1	(1)
Sapotaceae	*Synsepalum stipulatum*				4	0,4	
Myrtaceae	*Syzygium guineense*	water-berry, rose apple, bicoloured waterberry	Sumsum		1	0,1	(4)
Myrtaceae	*Syzygium guineense var. macrocarpum*		Buneji	Cika kondo	1	0,1	
Apocynaceae	*Tabernaemontana [pachysiphon ?]*	cow-tree, giant pinwheel flower			2	0,2	
Combretaceae	*Terminalia*		Kulahi	Bauche	5	0,6	
Combretaceae	*Terminalia avicennioides*		Kulahi	Bauche	15	1,7	(1)
Combretaceae	*Terminalia glaucescens*		Kulahi	Bauche	3	0,3	
Combretaceae	*Strephonema mannii*		Kom		32	3,6	
Sapotaceae	*Tieghemella heckelii*				1	0,1	
Moraceae	*Treculia*				3	0,3	
Moraceae	*Treculia obovoidea*				1	0,1	
Celtidaceae	*Trema orientalis*	trema, pigeon wood			1	0,1	(2)
Meliaceae	*Trichilia*		Kobahi		1	0,1	
Meliaceae	*Trichilia martineani*		Kobahi		55	6,2	
Meliaceae	*Trichilia splendida*		Kobahi		8	0,9	(1)
Euphorbiaceae	*Uapaca guinensis*	red cedar		Wawan kurmi	13	1,5	
Verbenaceae	*Vitex doniana*	black plum, West African plum	Ngalbije	Dinya	22	2,5	
Apocynaceae	*Voacanga africana*				3	0,3	
Annonaceae	*Xylopia staudi*	African pepper			2	0,2	(6)

(a) Internet-Sites used for verification of tree names (accessed 01-10Feb2010):
aluka.org (1), plantzafrica.com (2), worldagroforestrycentre.org (3), zimbabweflora.co.zw (4), zipcodezoo.com (5), wikipedia.org/en (6)

Trees and Vines in Forest and Savannah

Along the 8 km of straight-line transect at Kwano with its 984 labelled trees, 901 trees were taxonomically identified. The assemblage consists of 48 different families and 130–144 species (*Tab.03.05*). The number of specimens of a single species present on the transect varies considerably. About 40 % of all species are represented by a single specimen. The most common taxon Axlewood (*Anogeissus leiocarpus*) is represented with 61 individual trees. Half of all transect trees are made up by about 12 % of species, i.e. 16 different taxa (*Tab.03.06*).

Tab.03.06. Most common transect trees. Cumulatively, these species constitute half of all specimens

Family	Name	English name	Specimens on transect (n)	Specimens on transect (%)	Cumulative (%)
Anogeissus- Combretaceae	*Anogeissus leiocarpus*	axlewood	61	6.8	6.8
Trichilia - Meliaceae	*Trichilia martineani*		55	6.2	13.0
Crossopteryx - Rubiaceae	*Crossopteryx febrifuga*	African bark	49	5.5	18.5
Unknown	*Strephenoma manii*		32	3.6	22.0
Cola - Sterculiaceae	*Cola gigantea*	giant cola	30	3.4	25.4
Sterculia - Malvaceae	*Sterculia oblonga*	yellow sterculia	29	3.2	28.6
Bridelia- Euphorbiaceae	*Bridelia ferruginea*		28	3.1	31.8
Piliostigma - Caesalpinoideae	*Piliostigma thonningii*	camel foot	23	2.6	34.3
Vitex - Verbenaceae	*Vitex doniana*	black plum, West African plum	22	2.5	36.8
Bridelia- Euphorbiaceae	*Bridelia atroviridis*	rare forest bridelia	19	2.1	38.9
Bridelia- Euphorbiaceae	*Bridelia speciosa*		19	2.1	41.0
Hymenocardia - Euphorbiaceae	*Hymenocardia acida*		19	2.1	43.2
Lannea - Anacardiaceae	*Lannea acida*		19	2.1	45.3
Pseudospondias - Anacardiaceae	*Pseudospondias microcarpa*	African grape	19	2.1	47.4
Khaya - Meliaceae	*Khaya senegalensis*	African mahogany	16	1.8	49.2
Unknown	*Malacantha alnifola*		16	1.8	51.0
Sum			459		

Vines use trees for support by attaching themselves and climbing into the host tree canopy. About 50 % of transect trees are parasitized by woody climbers. The taxon "tiboko" of the genus *Landolphia* constitutes more than half of these plants (*Tab.03.07*). Numbers of climbers per transect tree were counted during two separate years. Their absolute prevalence dropped from 446 in the year 2002 (*Fig.03.04a*) to 372 in the year 2008 (*Fig.03.04b*). Nevertheless, in both instances did forest trees host significantly ($p < 0.001$) more vines (average = 1.0) than savannah trees (average = 0.2). The maximum number of vines hosted by a single tree was 7. One might expect that thicker trees host more vines. However, the number of woody climbers was not linked to the host tree's DBH (*Fig.03.05*).

Tab.03.07. Local names for woody climbers (aka “vine”, “liana”) growing on 985 transect trees. The most common taxon, "Tiboko", probably represents at least three species

Name (working term)	Specimens on transect (n)	Specimens on transect (%)	Cumulative (%)
Tiboko (*Landolphia* sp.)	239	57.3	57.3
Kimba	69	16.5	73.9
Maa pere (Fulani)	30	7.2	81.1
Quikusu (Gbaya)	15	3.6	84.7
Karkindam	9	2.2	86.8
Bungabingi	8	1.9	88.7
Ngoro (Fulani)	8	1.9	90.6
Bambami	6	1.4	92.1
Bangabingi	5	1.2	93.3
Bumbumi	5	1.2	94.5
Bumbumalo	4	1.0	95.4
Ndung	4	1.0	96.4
Gbambamalo	3	0.7	97.1
Kuli jei	3	0.7	97.8
Yasabia	3	0.7	98.6
Dargaza igiyar (Hausa), Gubuwol (Fulani)	2	0.5	99.0
Goro (Gbaya)	2	0.5	99.5
Dirmaje (Fulani)	1	0.2	99.8
Wank	1	0.2	100.0
Sum	417		

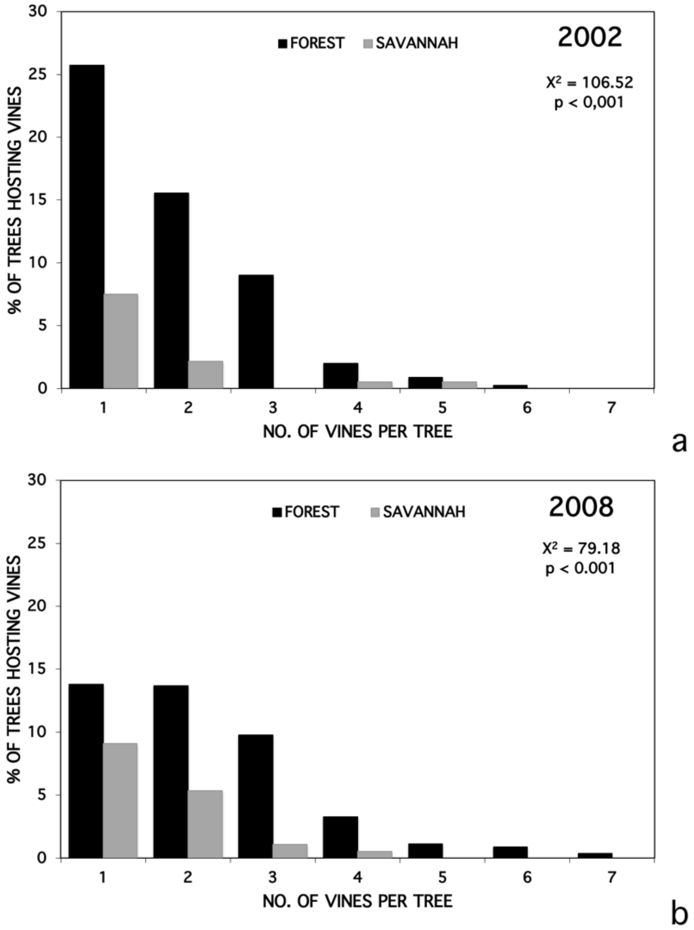


Fig.03.04. Vines per tree along the phenology transect. (a) During 2002 (Pearson’s Chi-squared test: $\chi^2(12) = 106.521$, $p < 0.001$ ***). (b) During 2008 (Pearson’s Chi-squared test: $\chi^2(7) = 79.184$, $p < 0.001$ ***). (2002 values from Fowler 2006: Fig.2.10)

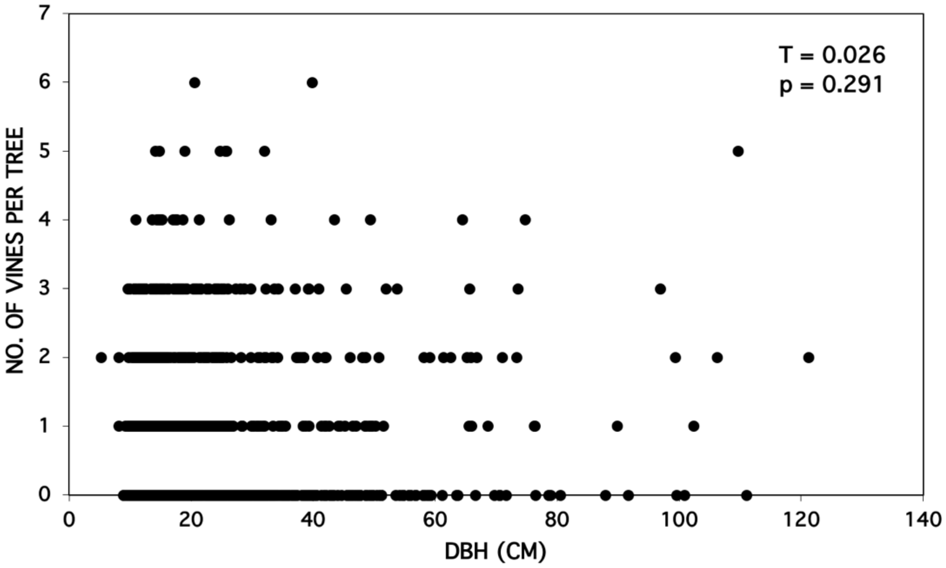


Fig.03.05. Vines per tree as a function of host-tree DBH (diameter at breast height) (Kendall's rank correlation Tau: T = 0.026, p = 0.291 ns)

As for tree height, a significant positive linear regression with logDBH was ascertained ($p < 0.001$, *Fig.03.06*) in that higher trees had thicker trunks. As for trunk girth, some clear differences between forest and savannah trees exist. Forest trees not only reach larger absolute DBH values (> 100 cm, maximum 117 cm), but the forest has also a clear predominance (> 50 %) of thinner trees (11–20 cm DBH). Savannah trees do not grow thicker than 80 cm DBH, but are more evenly distributed in the 11–40 cm range (*Fig.03.07*).

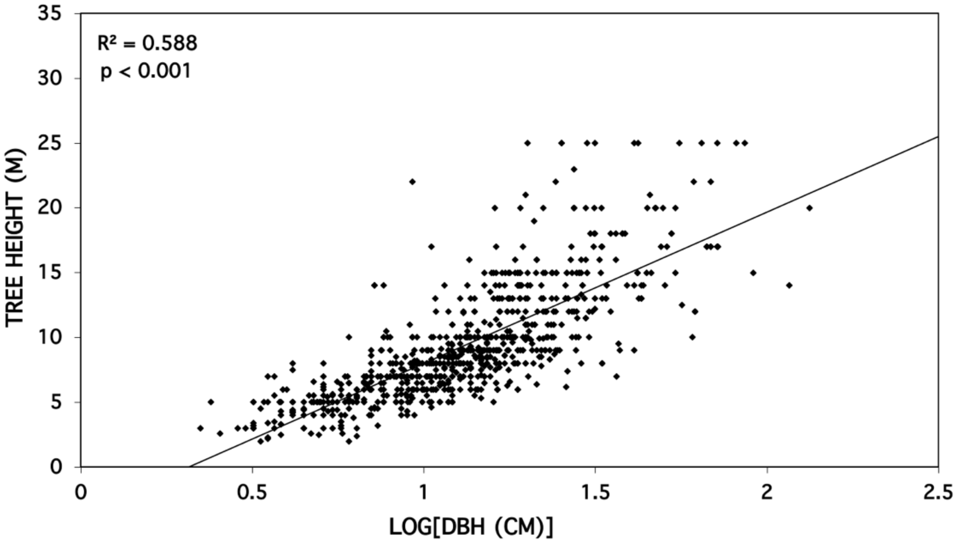


Fig.03.06. Tree height estimates as a function of Log(DBH) (Single linear regression: $F(1,835) = 1190$, $p < 0.001$ ***, $R^2 = 0.588$). Based on data for 837 chimpanzee nesting trees at Kwano (2002–2005). (Data collected by Andrew Fowler)

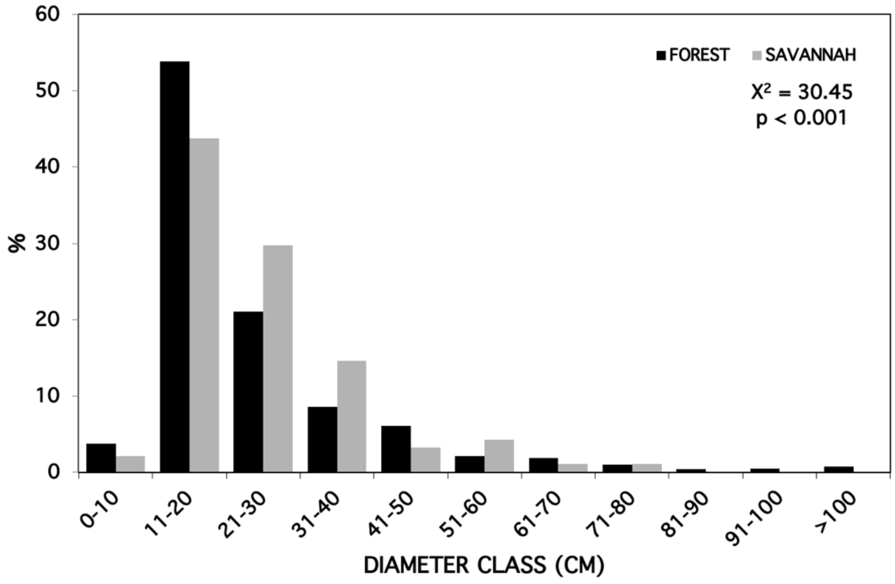


Fig.03.07. DBH of transect trees growing in savannah and forest segments (Pearson's Chi-squared test: $\chi^2(4) = 30.445$, $p < 0.001$ ***)

More than half of the transect trees had a DBH of 11–20 cm and only 14 % reached more than 40 cm. This pattern is even clearer when the 10 most common transect species are considered, where 3 species *(Bridelia ferruginea, Trichilia martineani, Piliostigma thonningii)* have more than 70 % of their representatives within the 11–20 cm range (*Fig.03.08*).

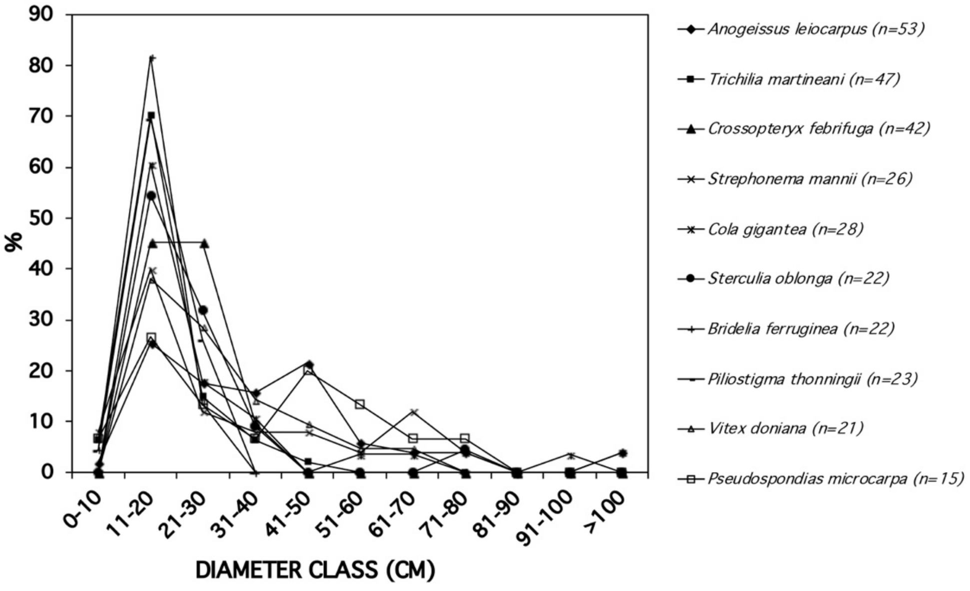


Fig.03.08. DBH categories of 10 most common transect tree species

Some tree species exclusively grow in forests, whereas others seem to flourish relatively more in one than the other type of habitat (*Tab.03.08*). Overall, 3 species are exclusive forest dwellers (*Cola gigantea*, *Pseudospondias microcarpa*, *Strephonema mannii*), while 4 others have more than 90 % of specimens within forests. The picture is somewhat different for savannah trees, where only a single species (*Crossopteryx febrifuga*) has more than three quarters of its specimens in that habitat alone.

Tab.03.08. Common species that grow predominantly (>50 %) in either forest or savannah parts of the transect

Species	n	Forest (n)	Savannah (n)	Forest (%)	Savannah (%)
Crossopteryx febrifuga	42	9	33	21.4	78.6
Piliostigma thonningii	23	11	12	47.8	52.2
Bridelia ferruginea	22	19	3	86.4	13.6
Anogeissus leiocarpus	51	46	5	90.2	9.8
Sterculia oblonga	22	20	2	90.9	9.1
Vitex doniana	21	20	1	95.2	4.8
Trichilia martineani	47	45	2	95.7	4.3
Cola gigantea	28	28	0	100.0	0.0
Pseudospondias microcarpa	15	15	0	100.0	0.0
Strephonema mannii	26	26	0	100.0	0.0

The Kwano study area consists of a mosaic of savannah and forest patches, which is reflected in the composition of 25-m segments along the 8 km transect (*Fig.03.09*). Forest dominates overall, notwithstanding that one 2-km transect stretch is predominantly populated by savannah trees. The overall proportion for the 320 segments is 27.8 % savannah (n = 89) against 72.2 % forest (n = 231).

As for tree density, those in forests are generally less spaced out, because the canopy of more than 80 % of specimens overshadows a ground area of less than 50 m^2. This reflects a highly significant difference to savannah trees ($p < 0.001$), which are far more spread out from each other (*Fig.03.10*). The average ground area occupied by a single savannah tree (48 m^2) was also significantly different ($p = 0.002$) from the ground area per tree in forest patches (31 m^2; *Tab.03.09*) – a finding that quantifies the qualitative differences between "open" and "closed" habitats.

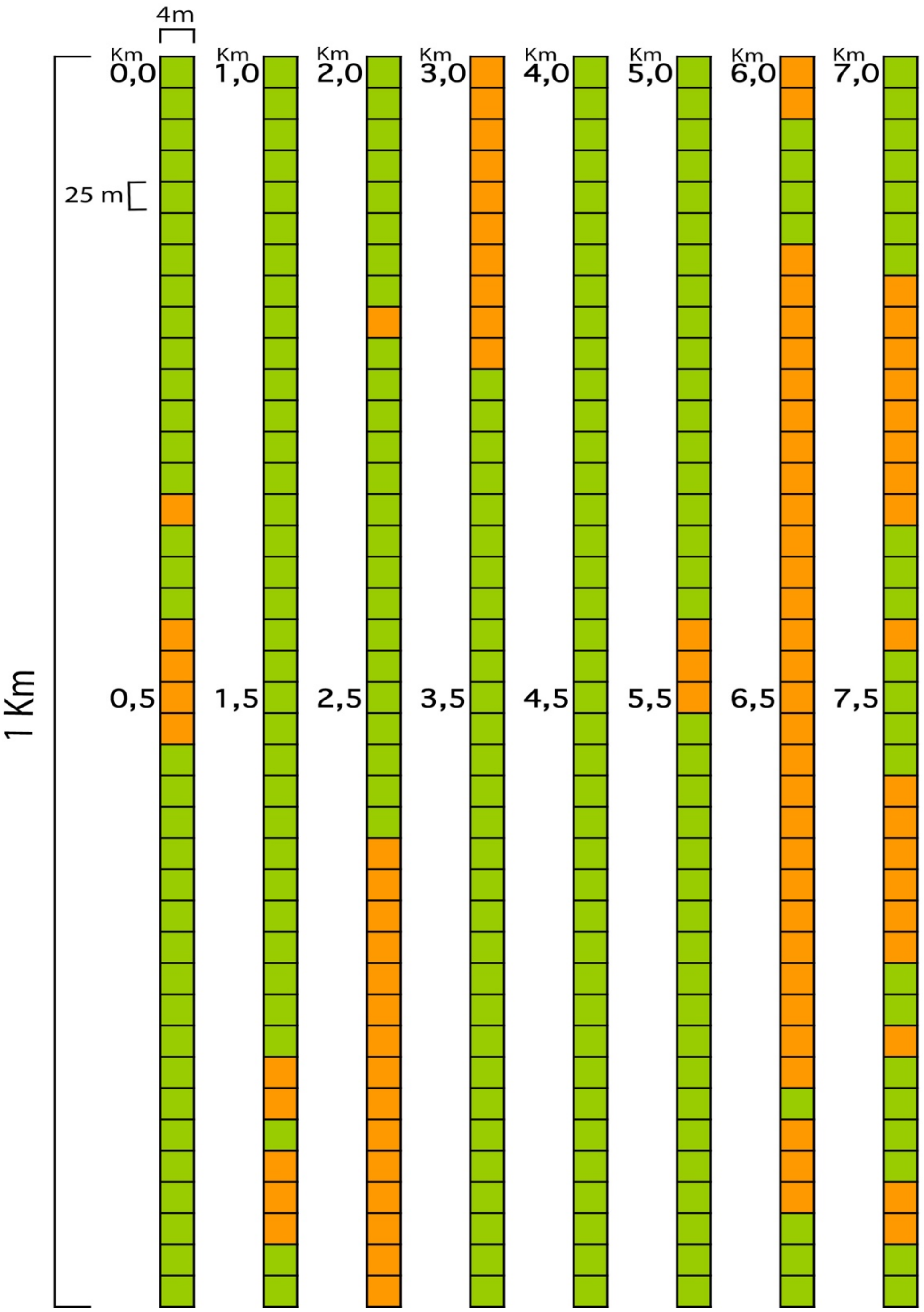


Fig.03.09. Succession of open savannah (orange squares) and closed forest (green squares) segments along the transect. Individual data points were recorded at each 50-m interval (0, 25, 50, 75, 100, 125, 150 m, [...] 7950, 7975, 8000 m)

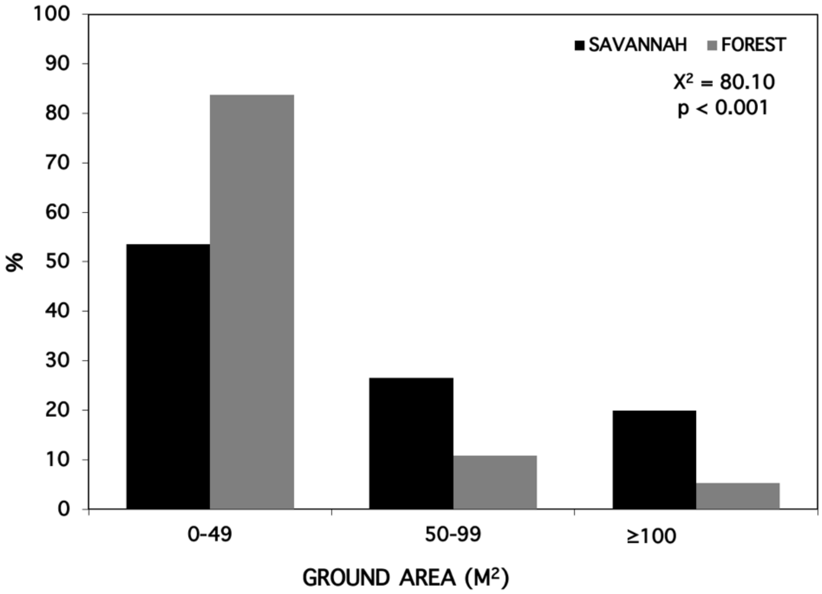


Fig.03.10. Tree density categories as measured via ground area occupied by transect trees in savannah compared to forest (see text for methodology) (Pearson's Chi-squared test: $\chi^2(2) = 80.104$, $p < 0.001$ ***)

Tab.03.09. Tree density averages as measured via ground area occupied by transect trees in savannah compared to forest (Wilcoxon rank sum test: W = 0.868, $p = 0.002$ **)

	Forest	Savannah	
Mean	30.6	47.9	**
Median	25.0	33.3	
Minimum	5.9	16.7	
Maximum	100.0	100.0	
Standard Error	0.69	2.1	
Count	801	181	

Flowering and Flushing Cycles

The study area harbours numerous types of blossoming plants (*Fig.03.11*). However, flower production is clearly more prevalent during the drier months (Nov–Mar) (*Fig.03.12*). In fact, a highly significant negative correlation exists between the percentage of flowering plants and monthly rainfall ($p < 0.001$, *Fig.03.13*).

Trees and climbers are also affected by the dry season in such a way, that they have fewer leaves (*Fig.03.14*). Nevertheless, this profound effect does not translate into significant positive correlation between flowering frequency and proportions of leafless transect plants (*Fig.03.15*).

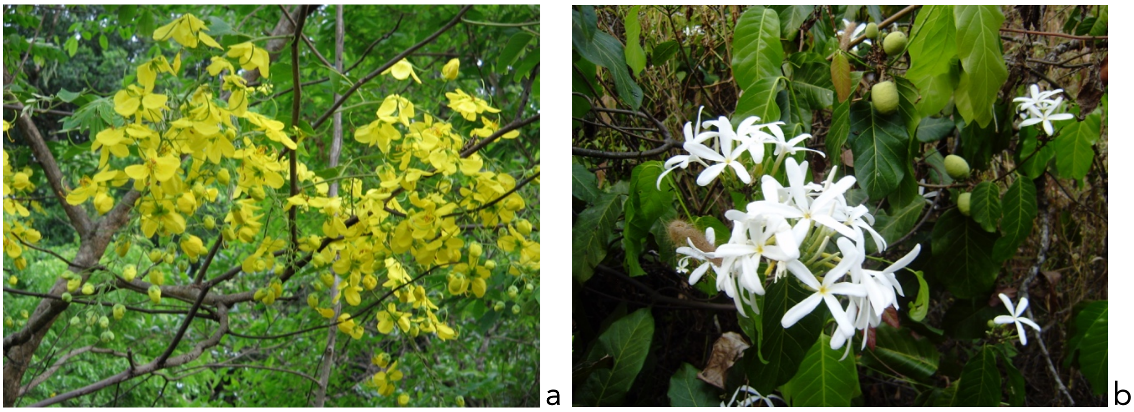


Fig.03.11. Flowers of exemplary transect plants. (a) *Parkia biglobosa*, the locust bean tree. (b) *Tabernaemontana pachysiphon*, the giant pinwheel flower. (Photos: Volker Sommer)

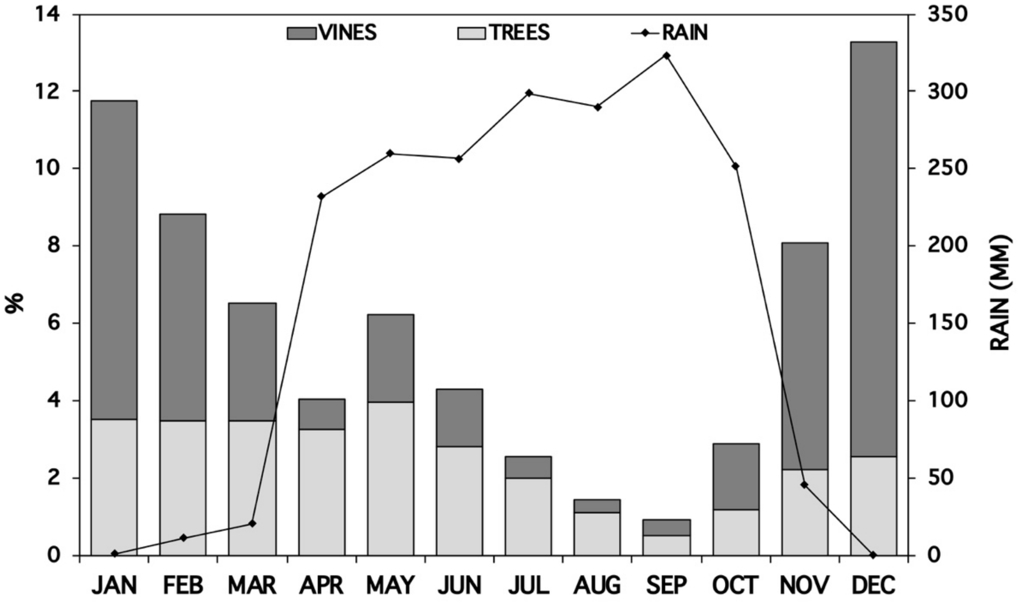


Fig.03.12. Annual rainfall and flowering schedule of transect plants. Data for Apr02–Jun09

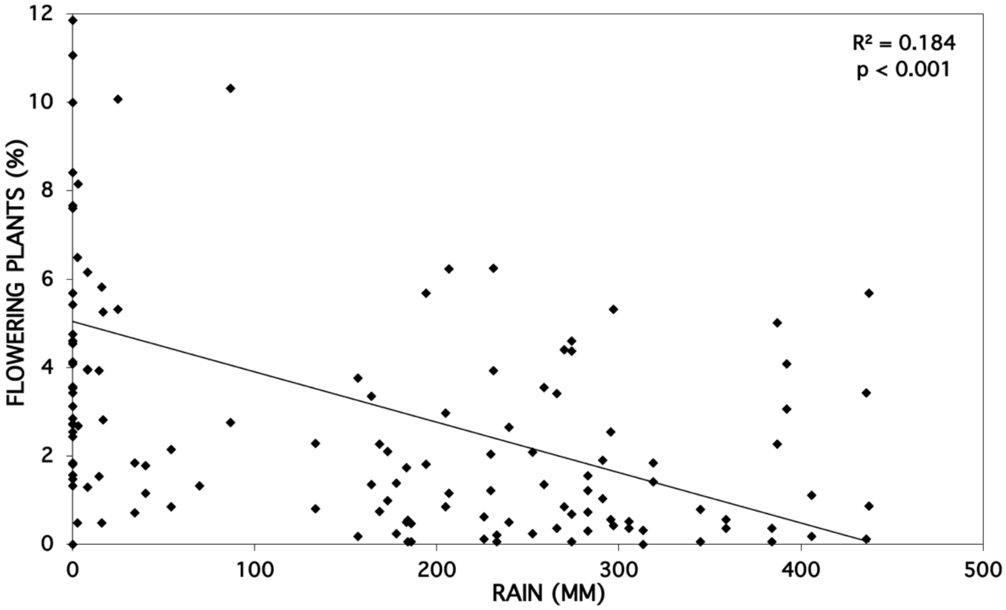


Fig.03.13. Monthly percentages of flowering transect plants as a function of monthly rainfall (Single linear regression: F(1,136) = 30.7, $p < 0.001$ ***, $R^2 = 0.184$). Data for Apr02–Jun09

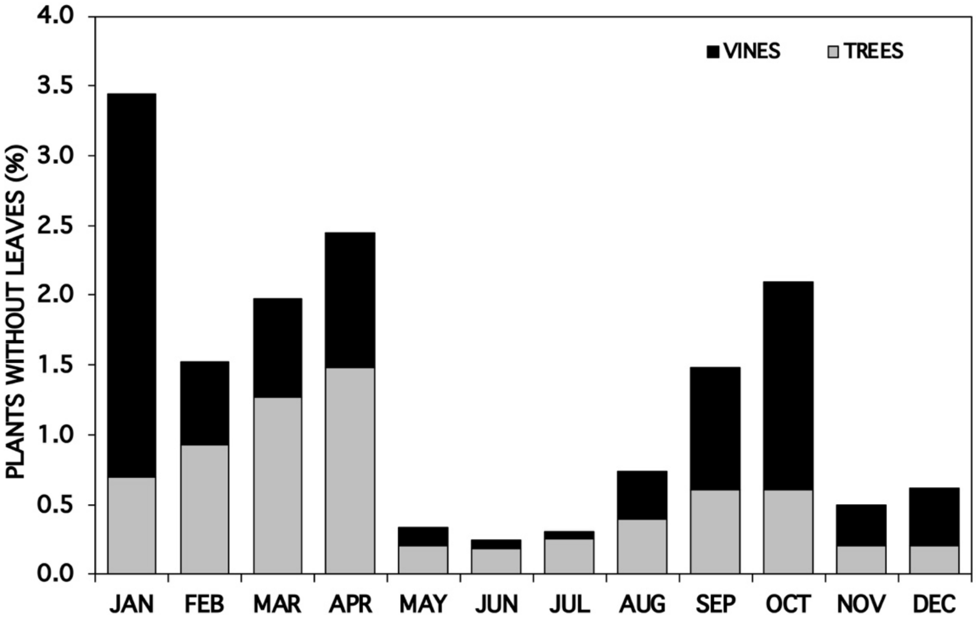


Fig.03.14. Percentage of transect plants not bearing leaves. Data for Apr02–Jun09

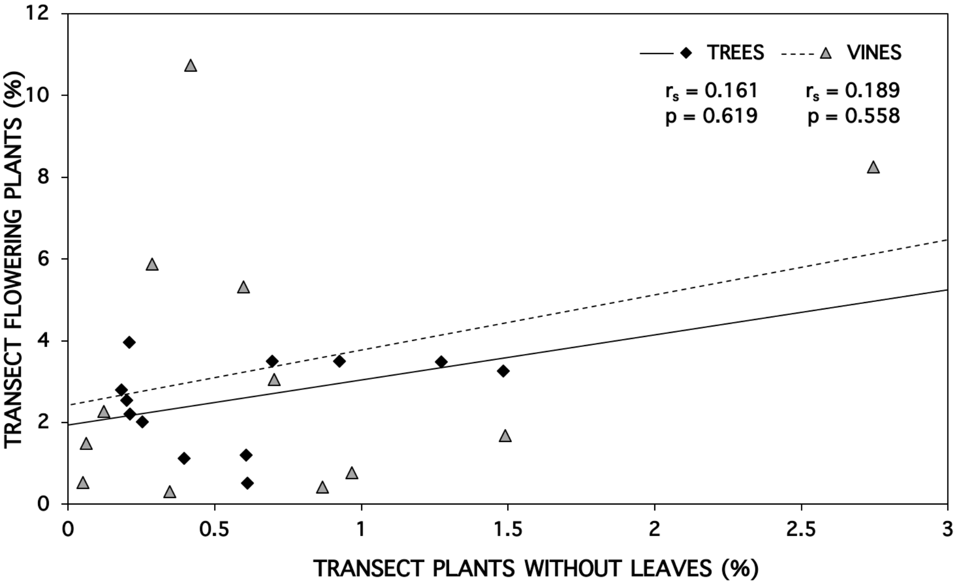


Fig.03.15. Correlation of the percentage of transect flowering plants with the percentage of transect plants without leaves (Spearman's rank-order correlation: Trees $r_s = 0.161$, $p = 0.619$ ns; Vines $r_s = 0.189$, $p = 0.558$)

Fruit Production

As already mentioned (see above, *Material and Methods*), fruiting of transect trees was recorded in a presence / absence method. Thus, this frequency is not necessarily equivalent with the amount of fruit available, given that plants, depending on species, crown size, age and reproductive state, may produce more or less or larger or smaller fruits. Nevertheless, these factors are likely evened out through the large sample of plants. In any case, two different measurements were used as proxies, i.e. the simple percentages of fruiting transect plants as well as the sum of the DBH of trees that bear fruits or harbour fruit-bearing vines (*fruit index*).

Fig.03.16. Ripening fruits. (a) The most common vine, *Landolphia sp*. (Tiboko; Apr13). (b) *Ficus* tree (Mar12). (Photos: Volker Sommer)

Fruits can be found year-round in the habitat as revealed by the pattern of fruit production of vines and trees (*Fig.03.16*). During any given month, an average of 8.1 % of the 1,799 transect plants are fruiting, i.e. 146 trees or vines (*Tab.03.10a*). However, there is a distinct seasonal cycle, with higher percentages from Mar–Jun, i.e. during the end of the dry season and the beginning of the rains. During that time, fruit production is accentuated, with higher fruit indexes scored (maximum of 5,741 in Apr09) (*Tab.03.10b*). Conversely, the lowest indexes are scored during the early dry season (minimum of 327 in Nov10). During the distinct peak from Mar–Jun, twice as many plants fruit than during the subsequent months from Jul–Dec (*Fig.03.17*). Such seasonal pattern is driven mostly by a considerable variation in vine fruit production. *Landolphia* taxa in particular swamp the forest with fruit from Mar–Jun. Trees, on the other hand, fruit with more or less the same frequency throughout the year. The two fruit-production measurements yielded similar results, with almost identical distribution curves (*Fig.03.18*).

Tab.03.10. Fruit productivity of trees (n = 984) and associated vines (n = 815) on the 8-km straight line transect in the Kwano habitat. (a) Percentage of fruiting plants during any given month. (b) Fruit index (sum of DBH of fruiting plants; in case of vines, the host tree's DBH was used)

(a) Fruit-bearing transect plants (%)

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2002(i)				13	13	9	5	6	12	12	7	6
2003(i)	5	4	14	12			3	3	3	3	2	1
2004(i)	3	6	6	3								
2005	6	9	13	15	11	9	8	7	6	5	5	6
2006	13	8	11	15	8	11	6	6	6	5	7	3
2007	5	11	15	18	15	12	3	5	7	5	3	3
2008	3	12	15	15	16	13	3	5	5	4	4	5
2009(ii)	11	11	11	14	13	13						
2010	9	15	13	15	11	6	7	8	8	5	1	2
2011	6	7	11	10	11	7	8	9	10	7	8	6
2012	8	11	13	12	10	10	8	9	5	6	6	2
Average	7	9	12	13	12	10	6	6	7	6	5	4

(b) Fruit index

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2002				3339	3295	2262	1336	1529	3047	2970	1631	1531
2003	1227	1040	3549	3086			751	837	671	660	461	291
2004	864	1399	1434	869								
2005	1278	1941	2811	3177	2371	1900	1717	1504	1408	1152	1133	1392
2006	3450	2136	3071	3998	2197	2906	1724	1699	1677	1388	1909	891
2007	1286	2919	4013	4754	4047	3176	906	1268	1820	1444	682	837
2008	802	3740	4754	4703	4885	3864	967	1477	1524	1303	1223	1643
2009	4367	4488	4565	5741	5435	5348						
2010	2663	4673	3846	4574	3275	1736	1999	2523	2447	1504	327	731
2011	1543	1909	3021	2821	2848	1982	2095	2342	2738	1986	2150	1525
2012	3520	4419	5292	5015	4235	3994	3154	3785	2110	2619	2311	986
Average	2100	2866	3636	3825	3621	3019	1628	1885	1938	1670	1314	1092

(i) Average annual fruit index was used to calculate percentages

(ii) Annual fruit index for 2012 was used to calculate percentages

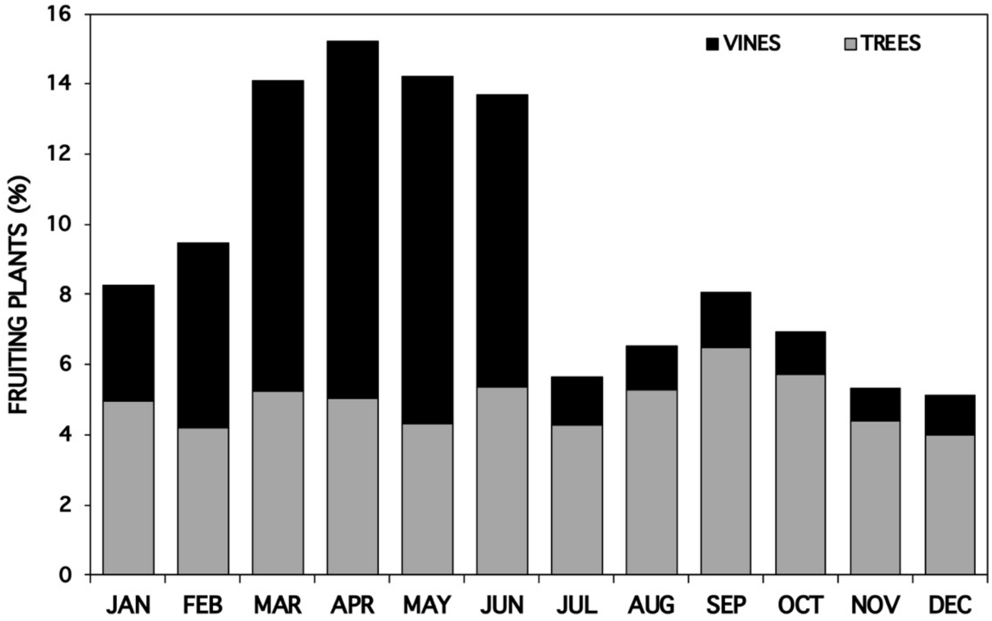


Fig.03.17. Fruit-bearing transect plants, including proportions of trees and vines. Data for Apr02–Dec12

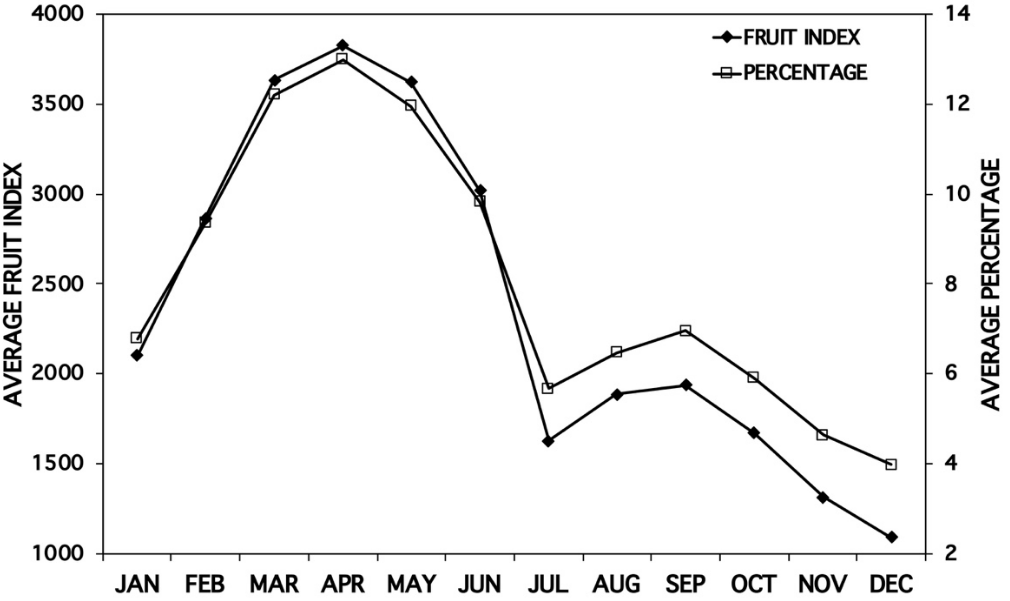


Fig.03.18. Comparison between fruit production measurements, i.e., values for fruit index and percentages of fruiting transect plants. Data for Apr02–Dec12

Throughout the 11 years of continuous records (2002–2012), fruit production followed the general yearly pattern very closely. This becomes obvious if we control for potential overall yearly fluctuations and transform the absolute fruit index (*Fig.03.19a*), into monthly percentages (*Fig.03.19b, Fig.03.19c*).

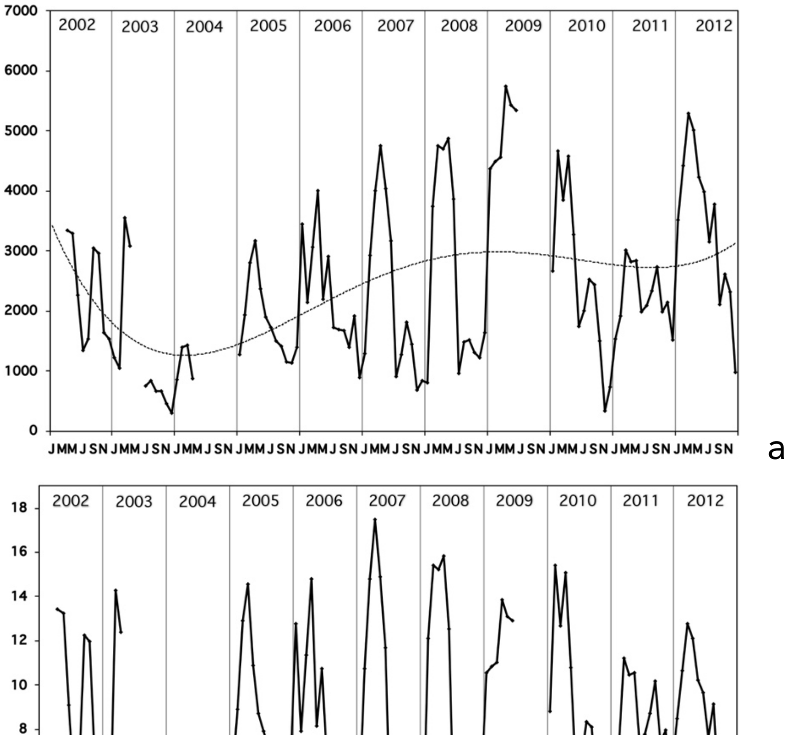


Fig.03.19. Yearly fluctuations of transect plant fruit productivity over an 11-year period (2002–2012). Various measures result in similar patterns. (a) Absolute fruit indices including polynomial trendline. (b) Monthly percentages of fruit indices (values for a given year set as 100 %). (c) Monthly percentages adjusted for a given year's maximum fruit index (i.e., month with highest index was set as 100 %)

Moreover, the long-term data allows to detect what is probably an underlying cycle of absolute fruit production that spans about a decade (*Fig.03.19a*). Thus, some years reach fruit indices as high as 41,440 (2012), while others have only half of that value with 21,789 (2005). The trend-line suggests that this wave-pattern repeats itself after a decade.

The spatial distribution of fruiting plants within the forest and savannah mosaic is not even, in that some areas are more suitable to carry a larger number of fruiting plants (e.g., gallery or lowland forests) than others (e.g., open woodland or grassland). This is revealed through a visual representation that takes the transects' spatial dimension into account and highlights patches with below- and above-average fruit production (*Fig.03.20*; for implications, see below, *Fig.04.22*).

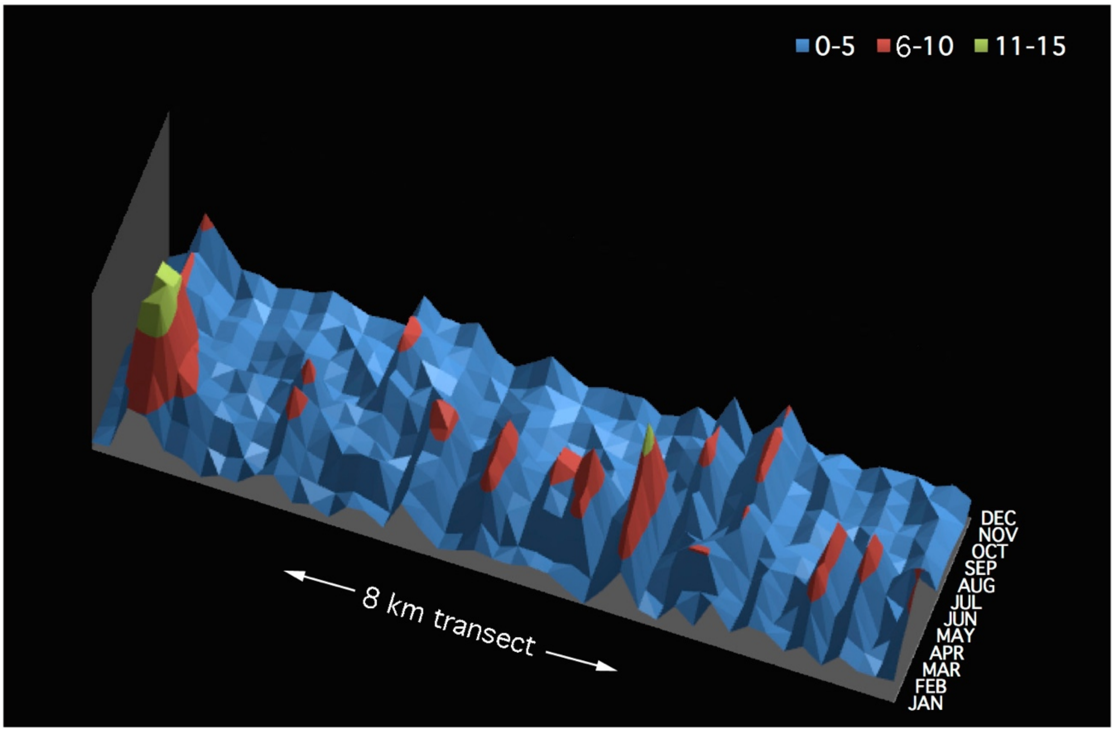


Fig.03.20. Fruit-bearing patches on the transect, measured via monthly numbers of fruiting plants on transect segments. The 8-km transect line was divided into segments of 150 m length. Temporal and spatial hotspots with 6–10 and 11–15 fruiting plants per month are highlighted in red and green. Data for Apr02–Jun09

Unlike flowering, seasonal fruit production is not significantly correlated with precipitation (cf. *Fig.03.02, Fig.03.13*), given that monthly rainfall is not a good predictor of fruit production (*Fig.03.21*).

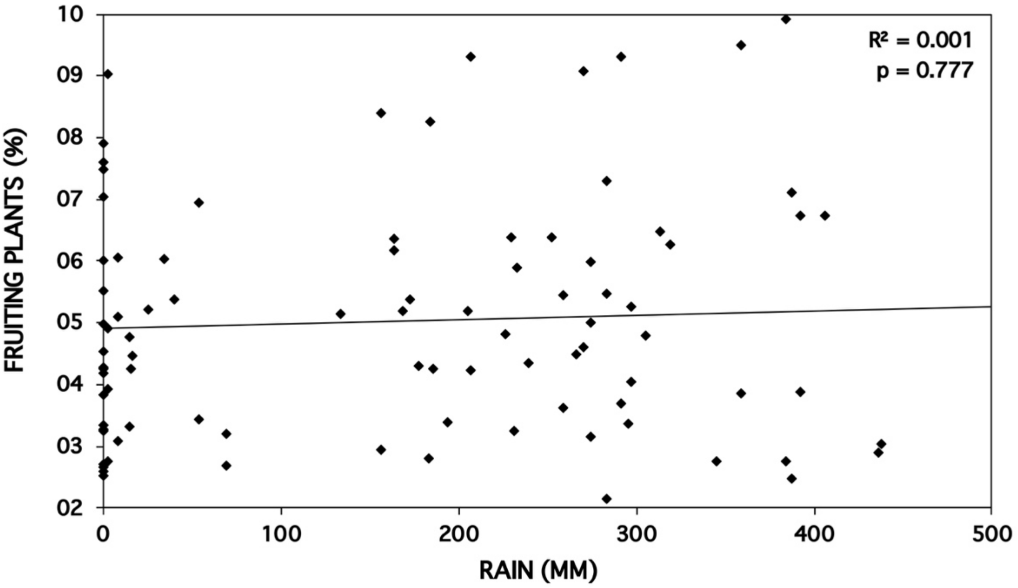
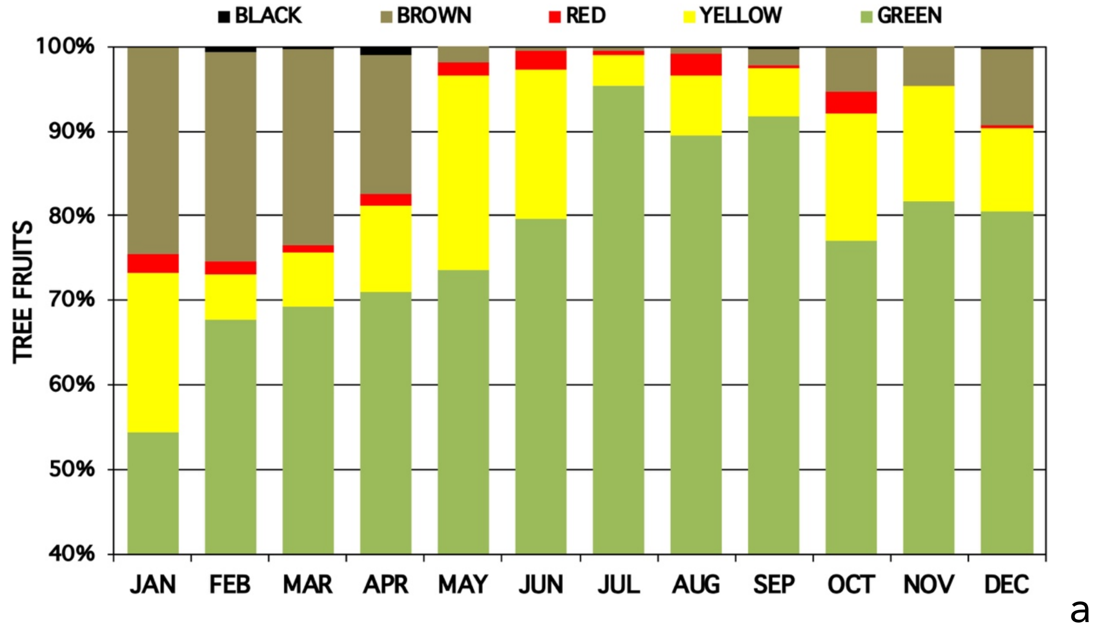


Fig.03.21. Percentage of fruiting transect plants as a function of rainfall (Single linear regression: F(1,136) = 0.080, $p = 0.777$ ns, $R^2 = 0.0006$). Data for Apr02–Jun09

Still, additional indication of seasonality was found with respect to the colouration of fruits. Green fruits dominate the spectrum for both trees and vines. However, trees have the largest proportions of green fruit during the rainy season, while non-green colours increase during the dry season (*Fig.03.22a*). In contrast, vines (*Fig.03.22b*) have a much smaller percentage of non-green fruits overall, with May–Jun constituting an exception. Brown vine fruits are much rarer than brown tree fruits, while both vines and trees produce only a few red coloured fruits. The classification of fruits into ripe / unripe closely follows this pattern, in that green fruits represent the less ripe stage (*Fig.03.23a*, *Fig.03.23b*).



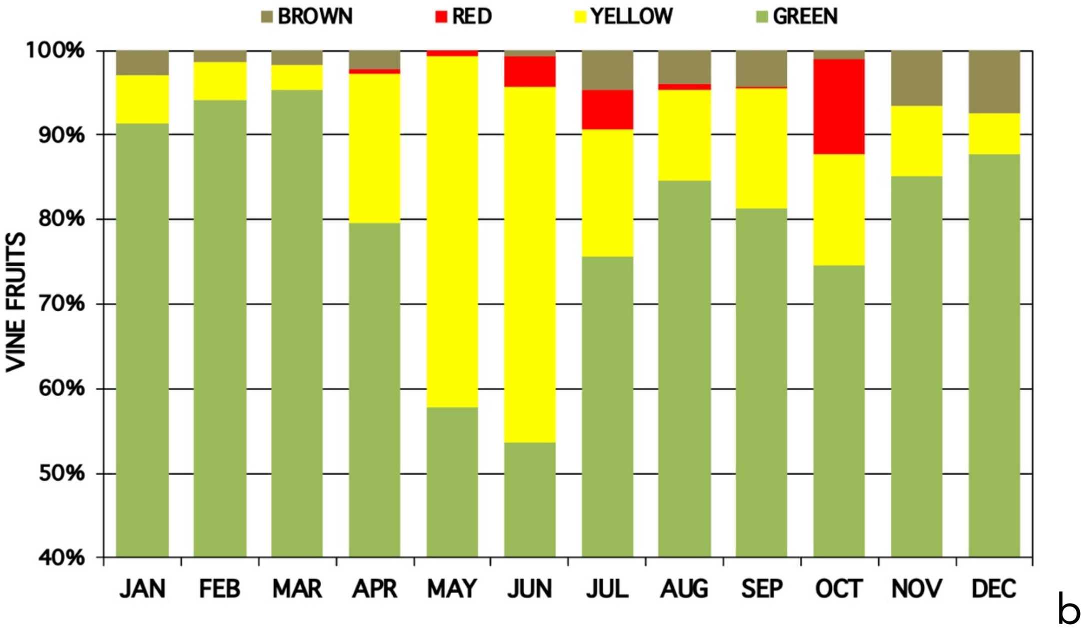


Fig.03.22. Colour of transect plant fruits (black, brown, red, yellow, green). (a) Tree fruits. (b) Vine fruits. Data for Apr02–Jun09

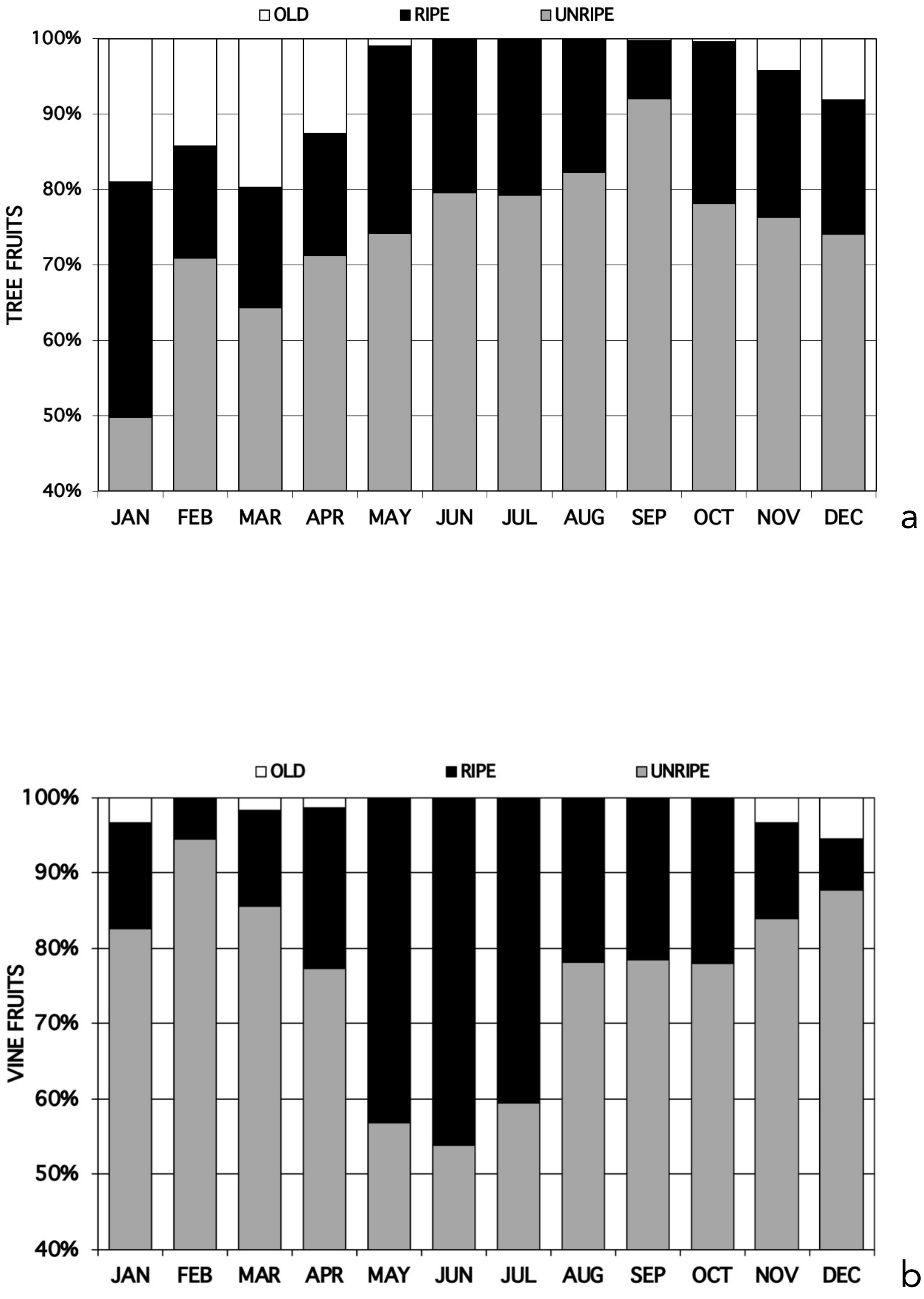


Fig.03.23. Ripeness of fruits found on transect plants. (a) Tree fruits. (b) Vine fruits. Data for Apr02–Jun09

Feeding Activity of Frugivores

Fruit production can be expected to be linked to the activities of frugivorous animals. Thus, feeding remains on the forest floor left by fruit-eaters, both terrestrial as well as non-terrestrial (arboreal, flying), are mostly found during months right after when fruit availability had peaked (*Fig.03.24*). This pattern is reflected in a highly significant positive correlation ($p < 0.001$, *Fig.03.25*).

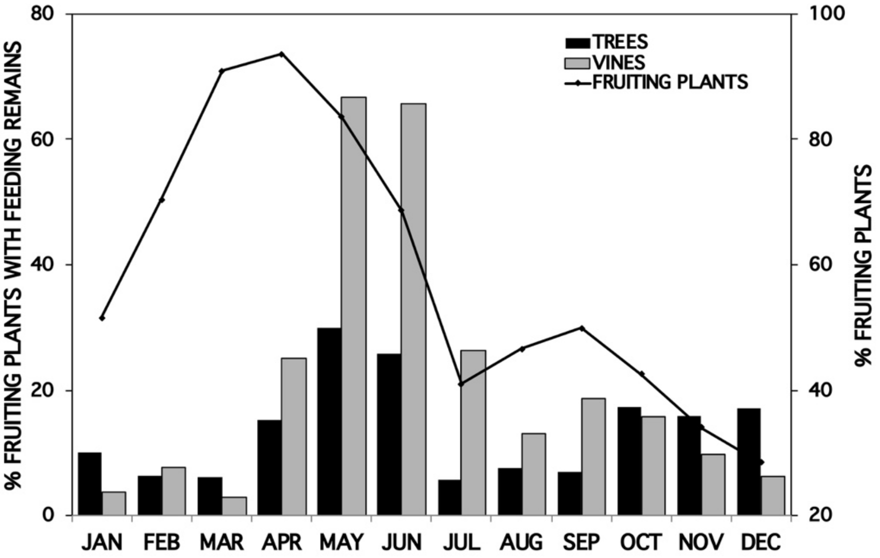


Fig.03.24. Percentages of fruiting transect plants under which feeding remains were found, broken down into trees and vines. Monthly overall percentages of fruiting transect plants provided as reference. Data for Apr02–Jun09

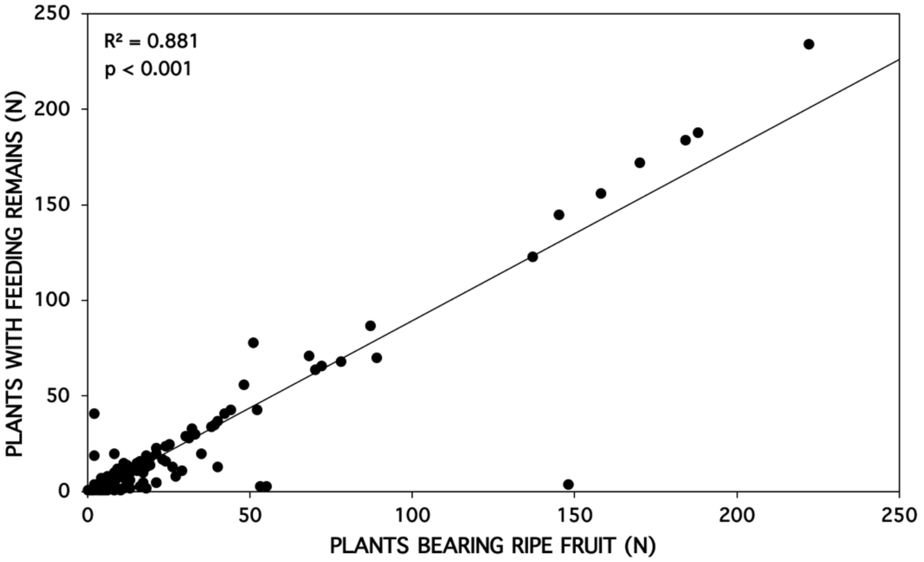


Fig.03.25. Number of transect plants under which feeding remains were found as a function of transect plants bearing ripe fruit (Single linear regression: $F(1,117) = 702.1$, $p < 0.001$***, $R^2 = 0.857$)

Primates can collect fruit directly from branches and, as a group, may well consume the largest amounts of any animal taxa. This is true at least with respect to identifiable feeding remains, given that fruit parts dropped by foraging monkeys and apes constitute at least half of all remains found under trees during 5 out of 12 individual months (*Fig.03.26*).

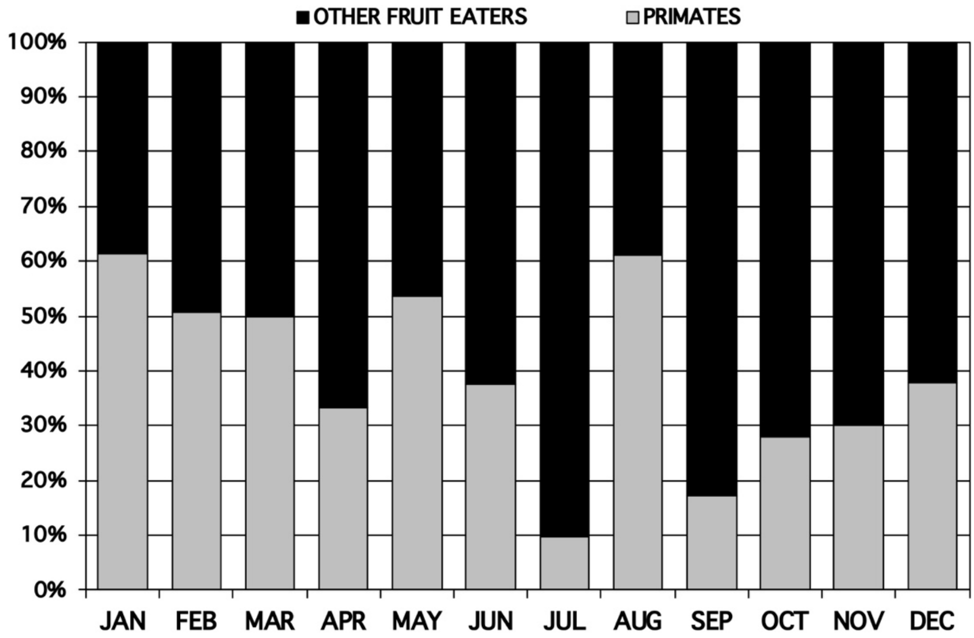


Fig.03.26. Who is consuming fruit? Proportions of primates versus other frugivores, as assessed from feeding remains. Monthly means, averaged across transect data for Apr02–Jun09. (Arboreal animals such as primates and squirrels may pick, partly eat and drop fruits; terrestrial mammals such as ungulates consume dropped and / or fallen fruits)

Polyspecific Associations of Monkeys

The four main monkey species inhabiting the Kwano study mingle more or less regularly (*Fig.03.27*). However, polyspecific associations are most commonly formed by mona monkeys, who are seen half of the time with other primates, while baboons rarely mix with others. Most regularly, associations form between mona and putty-nosed monkeys.

The frequency of polyspecific associations peak when trees and vines produce most fruit (*Fig.03.28*), although this positive correlation does not quite reach statistical significance (*Fig.03.29*).

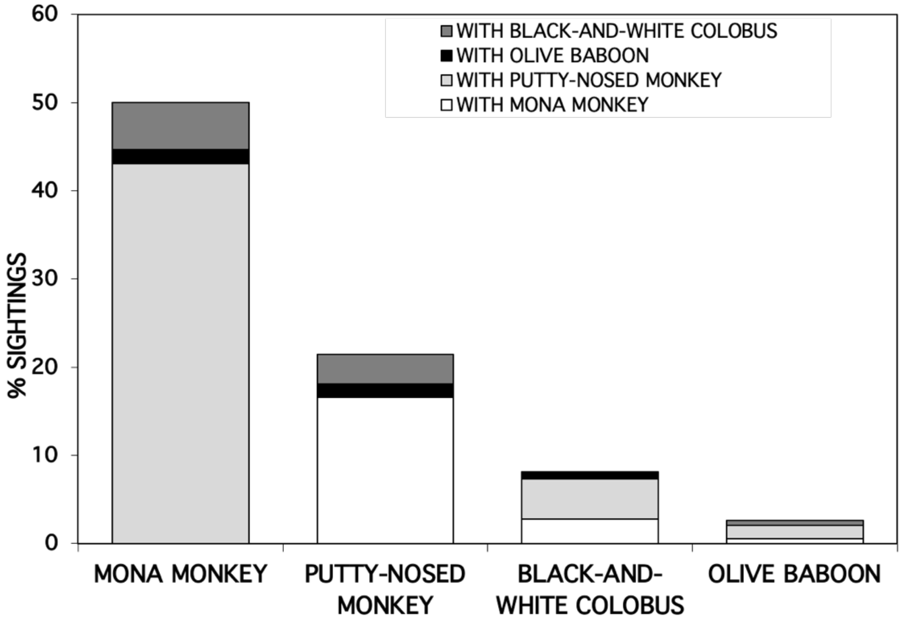


Fig.03.27. Polyspecific associations formed by monkeys. Based on foot surveys detailed in *Tab. 02.02*

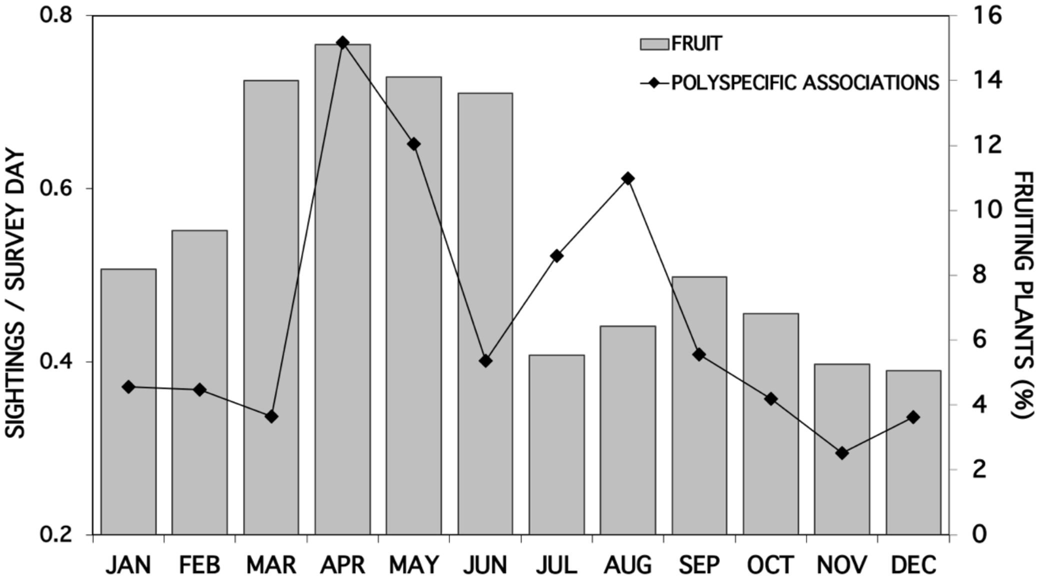


Fig. 03.28. Monthly distribution of polyspecific associations by monkeys compared to fruit availability. Rates indicate encounter probability during a hypothetical cumulative survey day of 13 h (06:00–18:00). Based on foot surveys detailed in *Tab. 02.02*

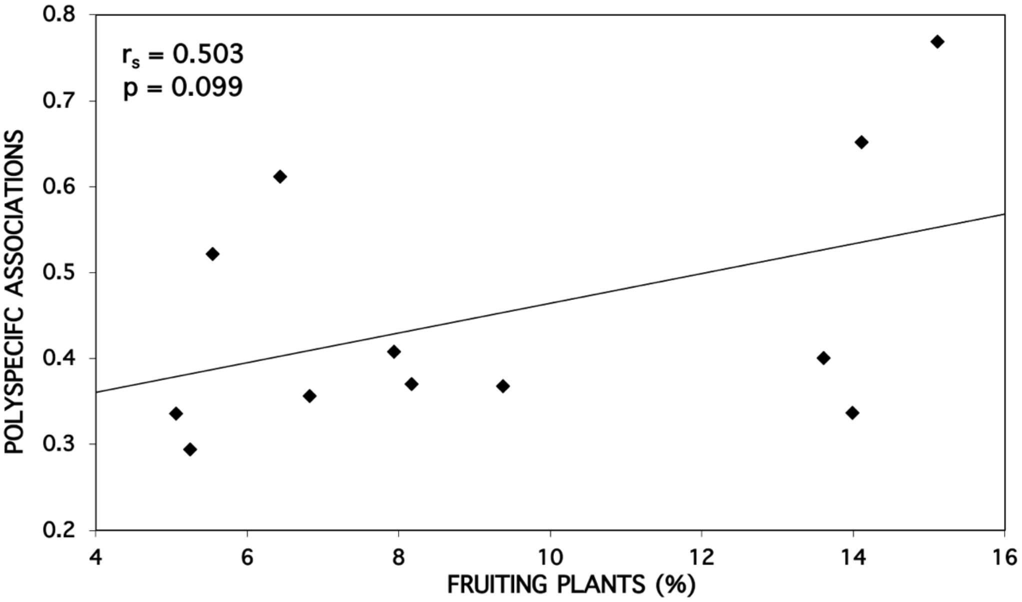


Fig. 03.29. Correlation between polyspecific associations formed by monkeys and fruit abundance. Measured as proportion of trees and vines fruiting on 8-km straight line transect, 2002–2009. Based on foot surveys detailed in *Tab. 02.02* (Spearman's rank-order correlation: $r_s = 0.503$, $p = 0.099$ ns)

DISCUSSION

Phenology data sets spanning across many years are rare in the tropics, a fact that constrains our ability to evaluate the degrees and potential causes of inter-annual variation and, even more complex, possible changes over decades (Chapman *et al.* 2005). Still, even without a pan-African perspective, ecological records on climate and phenology of the Gashaka study sites have a value in itself, given that few quantitative data exist about GGNP, one of Nigeria's last large nature reserves. However, within the remits of this research, the data also provide important background information with respect to their influence on the park's wildlife, and primates in particular (*Ch. 04–Ch. 06*).

Climate

Weather data for the study sites are probably the most detailed available for north-eastern Nigeria in general, given that record-keeping elsewhere is almost non-existent. According to this 13-yr data set, GGNP's Gashaka sector is characterized by seven months of wet season (Apr–Oct) followed by five months of dry season (Nov–Mar) (cf. *Fig.03.03, Tab.03.02*). Even though technically considered part of the Guinea savannah zone – although at its extreme eastern edge –, annual rainfall at the two study sites is higher than expected for this ecoregion and comparable to that of moister areas of tropical seasonally dry forests. This is likely related to the mountainous landscape with nearby elevations approaching 2500 m.

The habitat is a mosaic of semi-deciduous forests and savannah-woodland of anthropogenic making, as it is seasonally set on fire. Still, the Kwano site is less prone to such interference than the Gamgam site, given that the latter includes settlements around the village of Gashaka. As a result, there is more open habitat, including cultivated fields.

As for the two study sites, the overall similarity in the weather data comes as no surprise, given that the locales are only about 8 km apart. Still, slight differences may also be expected as the Kwano habitat lies 263 m higher (Gamgam 320 m, Kwano 583 m), is more forested and wedged against a steep hill, while the Gamgam habitat extends on both sides of a major watercourse, the river Gamgam, and includes fields. Indeed, the Gamgam climate feels warmer and less humid than that of Kwano. This qualitative difference is reflected in most quantitative values (cf. *Tab.03.04*). Kwano sees about 5 % more rain (plus 105 mm), experiences higher monthly means for humidity in terms of minima (plus 12 %) and maxima (plus 6 %), has a cooler average temperature (minus 0.4 °C), a lower monthly maximum mean (minus 2.0 °C) and a lower monthly minimum mean (minus 2.2 °C). Given that temperatures drop by 1 °C for every 100-m gain in altitude, it was expected that this difference would be more pronounced, i.e. about 2.6 °C. However, the Gamgam environment probably experiences a cooling effect, as it encompasses the banks of the river Gamgam, which is a major watercourse, while only two small creeks cut through the Kwano habitat.

Fire Regime

The pronounced wet-dry climate seasonality impacts majorly on the vegetation cover (with discernible knock-on effects for animal behaviour; see *Ch. 04–Ch. 07*). Thus, the plant cover varies dramatically between the peaks of the wet season (Jul–Aug) and dry season (Feb–Mar; cf. *Fig.03.03*). Trees in the open savannah have to cope with extreme fluctuations between intense water flow, sometimes even floods, on the one hand, and extreme dryness and exposure to fire, on the other. Forest trees, given mutual shade and the sponge-like retaining of water in the soil, are less exposed to direct sunlight and water run-off.

At GGNP, humans (including park rangers, field assistants, passers-by) set vegetation on fire during "early burning" (around Nov-Dec) and "late burning" (around Feb-Mar). This is a habitual practice, even in parts of the park where no humans live and no domestic animals are entering. Reasons given for this practice state that burning spurns the growth of succulent young grass and leaves on bushes and trees – from which wild animals, in particular ungulates, may also benefit. Indeed, experimental comparisons elsewhere between burned and unburned plots indicate that "plant growth in the burned plots began early after the fire, but growth was then restricted until rain fell. Burning near the middle of the dry season increased aboveground biomass by almost 30 %. Moderate fire stimulated growth of perennial grasses, since they can produce new shoots in a few days and rapid growth occurred immediately following the first rainfall. Grasses in unburned plots took longer to respond and never caught-up" (Osborne 2000: 67–68).

Nevertheless, there are also negative consequences of the fire regime, in that the heat hardens the ground, facilitating erosion once rains set in, and that fires select for hardy, silica-rich grasses not palatable to animals. Moreover, new shoots after a fire often wilt or are grazed before they are able to restore below-ground reserves. If fires are set late in the dry season, they may jump from the open savannah into the forests, as the floor is also very dried out in this closed environment, killing non-fire resistant plants within the forest. In this way, forested areas are slowly but steadily converted into savannah each year. The long-term result is deforestation and habitat fragmentation by which forest patches become increasingly smaller and further apart from each other (Bond & van Wilgen 1996, Osborne 2000, Uhl 1988).

Unfortunately, the fire-regime creates a vicious circle. This is, because not burning the savannah could lead to an accumulation of dry biomass which, when ultimately catching fire, may generate so much heat that it would set even the canopy of wetter forest ablaze. This was a cause for the 1988 Yellowstone National Park fires in the USA. Here, fires were systematically suppressed for decades, as they were believed to be detrimental – which then facilitated a "catastrophic" burning event (Turner *et al.* 2003). It is thus likely that GGNP will continue to be subjected to human-made fires, a practice that, for better or worse, alters not only its floral, but also faunal composition (*Ch. 04*).

Trees

Data on tree diversity are restricted to one of the study sites, Kwano. In terms of its 8-km transect length, 72 % was classified as forest and 28 % as savannah-woodland (cf. *Fig.03.09*). The Gamgam site has certainly less forest, given its proximity to human settlements, which led to forest clearance for cultivation purposes and to construct human habitations, as well as the fact that it encompasses flood plains of the river Gamgam. Other parts of the national park have been subjected to large-scale deforestation and now consist of grassland, probably of anthropogenic origin (Gumnior & Sommer 2013).

As expected, forested parts of the study area were richer in terms of tree species composition than savannah patches. On the Kwano transect, 130–144 tree species were identified, although about 40 % of the taxa were represented by a single specimen (cf. *Tab.03.05*). Thus, the habitat's species richness is likely under-represented as many other rare trees might exist but not be captured by the transect line, despite its considerable extent. This is confirmed by the finding that the cumulative percent of new species discovered while walking the transect does not flatten even when the whole 8 km are taken into account (Fowler 2006: Fig.2.7). For example, some rather common trees such as *Prosopis africana* and *Milicia excelsa* are not represented on the transect.

These results are in line with the idea that rare species represented by only a few individuals are a major contributor to the overall diversity of rain forests (Osborne 2000). Fine-tuned, differential survival skills of various tree species might thus be at the heart of rain forest tree diversity, given the general lack of niche separation. The findings of the current study confirm the concern (Adamescu *et al*. 2018) that extensive, longitudinal datasets are necessary to understand general phenological cycles, not least to compensate for the considerably heterogeneity of individual tree responses (see also Chapman *et al*. 1999).

Vines

Forest trees tend to have more attached vines than savannah trees (cf. *Fig.03.04*), rendering woody plant diversity even higher in forests. On the other hand, more than half of all vines belong to the genus *Landolphia* (cf. *Tab.03.07*). Although not identified to species level, vine diversity seems to be low with only 19 different varieties, mostly identified by the local names, out of 417 individual specimens. Thus, one has to pass 6–7 transect trees (901 / 130–144) to come across a new taxon, whereas one has to pass 22 host trees (417 / 19) to come across a new type of vine.

Woody climbers compete with trees, reducing their growth, fruit production and increasing their mortality (Ingwell *et al.* 2010), although these factors were not investigated at the Kwano study site. Moreover, one might predict that thicker trees can "bear" more lianas, but this was not the case, as liana infestation proved to be independent from host-tree DBH (cf. *Fig.03.05*).

Many study area trees are deciduous, as indicated by the annual variation in transect plants who have shed all leaves (cf. *Fig.03.14*). Deciduous species are less able to compete with evergreens when water is freely available. However, in seasonal habitats, this dynamic is reversed, with trees better able to cope with water-scarce periods having an advantage (Osborne 2000). This probably explains the high frequency of semi-deciduous trees in the study area.

Diameter at breast height (DBH) has widely been used as a measurement to infer height, crown size, health and tree performance (Hemery *et al.* 2005). Contrary to the idea that many species do not exhibit a linear relation between height and diameter (Turner 2001), results for Kwano confirm other studies (Sumida 2015) that identified a positive relationship between DBH and height, (cf. *Fig.03.06*).

In forests, selected specimen may grow very large with DBH > 100 cm, while for savannah trees, 80 cm seems to be the cut-off. Overall, however, savannah trees had a higher proportion within the 21–60 cm range, whereas forests are dominated by thinner trees (11–30 cm) (cf. *Fig.03.07*). This most likely reflects two factors. First, forests have greater regeneration properties, given less disturbance from fire and grazers that allow for seedling growth; secondly, the greater density of trees in forests (cf. *Fig.03.10, Tab.03.09*) entails more competition for sunlight exposure, selecting for specimen that can grow tall at the expense of thickness.

Flowering

Angiosperm plants reproduce sexually via pollination, often aided by animals attracted to the flower's nectar who then carry pollen from one blossom to the other. While some flowers evolved in close association with a specific pollinator, others rely on opportunistic feeders (Osborne 2000), including numerous insects, birds or bats. It should be mentioned that primates can also act as pollinators, although their role has often been overlooked (Heymann 2011).

In at least some African forests, flowering activity peaked at the beginning or during the middle of one of the two wet seasons (Adamescu *et al*. 2018). This finding contrasts somewhat with the idea that, because rainfall decreases pollination chances (Turner 2001), it should be expected that angiosperms preferentially flower during dry periods. The data presented here for Kwano confirm the latter prediction as flowering takes place mostly outside the wet season (cf. *Fig.03.12, Fig.03.13*). Less humidity and rainfall as well as higher temperatures during the dry season (average maximum 32.2 °C, Nov–Mar) compared to the wet season (31.3 °C, Apr-Oct; cf. *Tab.03.03*) reduces the likelihood that pollen will be damp and stick together. Central American forests exhibit similar flowering pattern (Janzen 1967, Daubenmire 1972, Smith-Ramirez & Armesto 1994).

Flowering is often associated with periods of leaf fall, due to which blossoms become more conspicuous and easier to access for potential pollinators. However, our results did not ascertain that flowering peaks at Kwano coincide with periods when more trees are without leaves (cf. *Fig.03.14, Fig.03.15*).

The few existing detailed studies of African forests indicate that annual flowering cycles are the most common, notwithstanding that frequencies may vary from sub-annual to supra-annual (Adamescu *et al*. 2018). The current study, despite spanning more than a decade, largely works with an aggregated sample. It will be a task for the future to disentangle potential patterns of annual, sub-annual and supra-annual cycles, of both flowering and fruiting.

Fruiting

Fruit production in tropical forests varies seasonally (Tutin & Fernandez 1993). The results for the Kwano site confirm this, with very similar pattern obtained via two different calculations, i.e. percentage of fruiting plants on the transect resp. a fruit index based on the sum of the DBH of fruiting plants (cf. *Fig.03.18*).

However, while fruit production peaked between Mar–Jun, fruits are produced year-round, albeit often at lower frequency (cf. *Fig.03.17*, *Fig.03.18*). This is also illustrated by the graphic representation of fruiting peaks in different segments of the transect (cf. *Fig.03.20*), which are not restricted to the Mar-Jun peak period. Again, this finding is in concordance with those for other African forests (Chapman *et al*. 1999).

Despite the generally negative correlation between flowering and rainfall, this pattern did not translate into a correlation between fruit production and rainfall (cf. *Fig.03.21*) – indicating that the transect harbours plants whose fruits ripen with different speed.

More than trees, vine fruit production seems to drive fruiting seasonality (cf. *Fig.03.17*). A preponderance of the habitat's vines belongs to the genus *Landolphia* (cf. *Fig.03.16a*), which usually bear fruit from Mar–Jun. The high frequency of this plant is largely responsible for the peak in fruit availability during this transitional period between dry to rainy season. Unlike fruit on terminal branches, vine fruits are typically covered by the canopy and thus have restricted exposure to sunlight. The relatively restricted fruiting peak might reflect this and be triggered by the sunniest period of the year just before the onset of heavy rains (van Schaik & Pfannes 2005).

The same annual seasonal pattern was reconstructed year after year, albeit absolute fruit production might vary (cf. *Fig.03.19*). Thus, some years yielded more and others much less fruit. The variation in absolute numbers is unlikely to be an artefact, given that the same field assistants recorded the data. Instead, fruiting volume could be regulated by some climatic factor. Tutin & Fernandez (1993) point to the existence of a critical minimum temperature for fruit production, rather than the amount of rainfall. However, while mean minimum annual temperatures for Kwano (cf. *Tab.03.03*) fluctuate between 20–22 °C, there is no discernible pattern in relation to the minima or maxima of fruit production.

Further analyses of what seems like a cyclic nature of absolute volume of fruit production would be useful, particularly in relation to a potential synchronisation of fruiting by certain common species. Such masting could be a strategy to swamp seed predators (Visser *et al.* 2011). Thus, if prey items briefly occur at high densities, the probability is reduced that an individual organism will be eaten – the "predator satiation" effect behind the famous periodical cicadas (reviews in Molles 2002). Moreover, some other studies found that fruiting is more likely to exhibit supra-annual cycles than flowering. This may be caused by resource deficiencies, stochastic weather or disease, factors can prevent fruiting after a flowering event and thus modify annual cycles (Adamescu *et al.* 2018).

Fruit ripeness

Succulent fruits attract animals that feed on the fibrous and sugar-rich pulp, which typically envelops the seeds. Ripe fruit are generally thought to have a sweeter taste and to be more easily digestible, thus making them more desirable for frugivores. In addition, they tend to exhibit more conspicuous colours, which increases the probability that animals with colour vision (e.g., birds and primates) find them.

This study reveals a straight-forward link between colour and ripeness (cf. *Fig.03.22, Fig.03.23*). Thus, green fruits are usually unripe (but not always!), whereas red, yellow, brown and black typically indicate ripeness.

The time when fruit is ripe should be in line with optimal conditions for germination and seedling survival. However, if this is so, then trees and vines behave differently (cf. *Fig.03.22, Fig.03.23*). Tree fruits tend to be ripe during the dryer months, indicating that water availability during the peak rainy season may be an important abiotic factor for seed germination. Vines, on the other hand, are mostly ripe when the rains are setting in. Germination experiments would be needed to find out if perhaps *Landolphia* seeds germinate faster than tree seeds, so that these vine seeds would likewise germinate during the peak rains.

Fruit Eaters

Frugivorous animals are important for seed dispersal (zoochory) in that they may carry seeds far from the mother plant. In fact, some plant seeds will only germinate after passage through an animals' digestive tract (endozoochory) (Cavallero *et al.* 2012). Ripe fruit will more easily detach from its mother plant, either when manipulated by animals or through climatic factors such as wind and rain. Some animals can get the fruit straight from the plant, whereas others are confined to fallen fruit accumulating on the floor. Thus, seed dispersers are not restricted to arboreal animals that consume fruit right at the branches (e.g., primates, rodents, birds), but include animals that feed on dropped fruit (e.g., pigs, antelopes, civets).

However, far from being "dedicated" seed-dispersers, frugivorous animals can also destroy seeds when masticating fruit, either accidentally or on purpose. This is particularly true for ruminants and large rodents, who destroy the seeds of about 70 % of the species they feed on (Gautier-Hion 1990). Still, even these predators can inadvertently disperse seeds if they drop some or if they hoard seeds, leaving a few behind that will then germinate (Janzen 1971, Gautier-Hion *et al.* 1993).

The activity of frugivorous animals can be reconstructed by looking at feeding remains (cf. *Fig.03.25*), given that different kinds of animals produce different bite marks. Using this approach, primates were found to be the most prolific frugivores (cf. *Fig.03.26*). However, the fact that most feeding remains stemmed from primates may simply indicate that they are very messy eaters, dropping many of the fruit they are plucking from branches.

Phenology and Monkey Grouping Pattern

Changes in the availability of diet are expected to influence animal social organization (Chapman *et al*. 2017). These dynamics will not only cause variations at the intra-specific level (see Ch. 04, Ch. 05), but also inter-specific variation in how different taxa interact. A fitting example elucidated by the data of this study are polyspecific associations formed by the monkey species of the study site, the largely arboreal mona monkeys, putty-nosed monkeys, black-and-white colobus as well as semi-terrestrial baboons. These different monkey taxa can co-exist in large numbers through relatively obvious niche segregations (cf. *Tab. 03.11*). Black-and-white colobus are the most folivorous and arboreal taxon, whereas baboons represent the most omnivorous and least arboreal. Mona monkeys and putty-nosed monkeys, however, are relatively similar in terms of preferred canopy stratum and diet.

It therefore seems somewhat counterintuitive, that mona and putty-nosed monkeys form polyspecific associations most often (cf. *Fig. 03.27*). However, these are not continuous (although actual time budgets were not measured), and more fine-tuned niche separation might not have been captured by the rather rough categories. In any case, the relatively small monkeys experience considerable predation pressure (crowned eagles, leopards, probably golden cat; Arnold *et al.* 2011) – one assumed reason for the evolution of mixed-species associations that are not only common in many communities of primates, but also in those of fish or birds (Stensland *et al.* 2003). Often-cited anti-predatory benefits include safety in numbers (Noë & Bshary 1997, Eckardt & Zuberbühler 2004), cooperation in defence (McGraw & Zuberbühler 2008) as well as, in the first place, increased likelihood of detecting predators (Kenward 1978), especially if certain association partners are especially effective in raising the alarm (this includes putty-nosed monkeys, Noë & Bshary 1997).

The concurrent costs of increased feeding competition can theoretically be mitigated, if, on the other hand, polyspecific associations lead to a higher likelihood of finding or defending food patches (Buzzard 2010). Thus, other things being equal, one can expect lower frequencies of polyspecific association when less food is around – an effect clearly discernible at Kwano (cf. *Fig. 03.28, Fig. 03.29*).

Conclusion

The Gashaka area (and the Kwano study site in particular) is characterised by a mosaic of semi-deciduous forests interspersed with patches of Guinea savannah. These open habitats are most likely the consequence of a long-standing human fire regime. The vegetation cover is heavily influenced by a distinct climatic seasonality, with 5 months of dry season with virtually no rain followed by often hefty downpours from mid-Apr to mid-Nov that constitute 97 % of all precipitation. Phenological events of trees and vines (flowering, leafing, fruiting) closely correlate with the alternation between a wet and dry season. Hence, it is expected that these patterns are also highly significant for the biology and behaviour of wildlife in the area, including non-human primates.

CHAPTER 04

CHIMPANZEE GREGARIOUSNESS.

INFLUENCE OF ABUNDANCE AND DISPERSION OF FOOD PATCHES

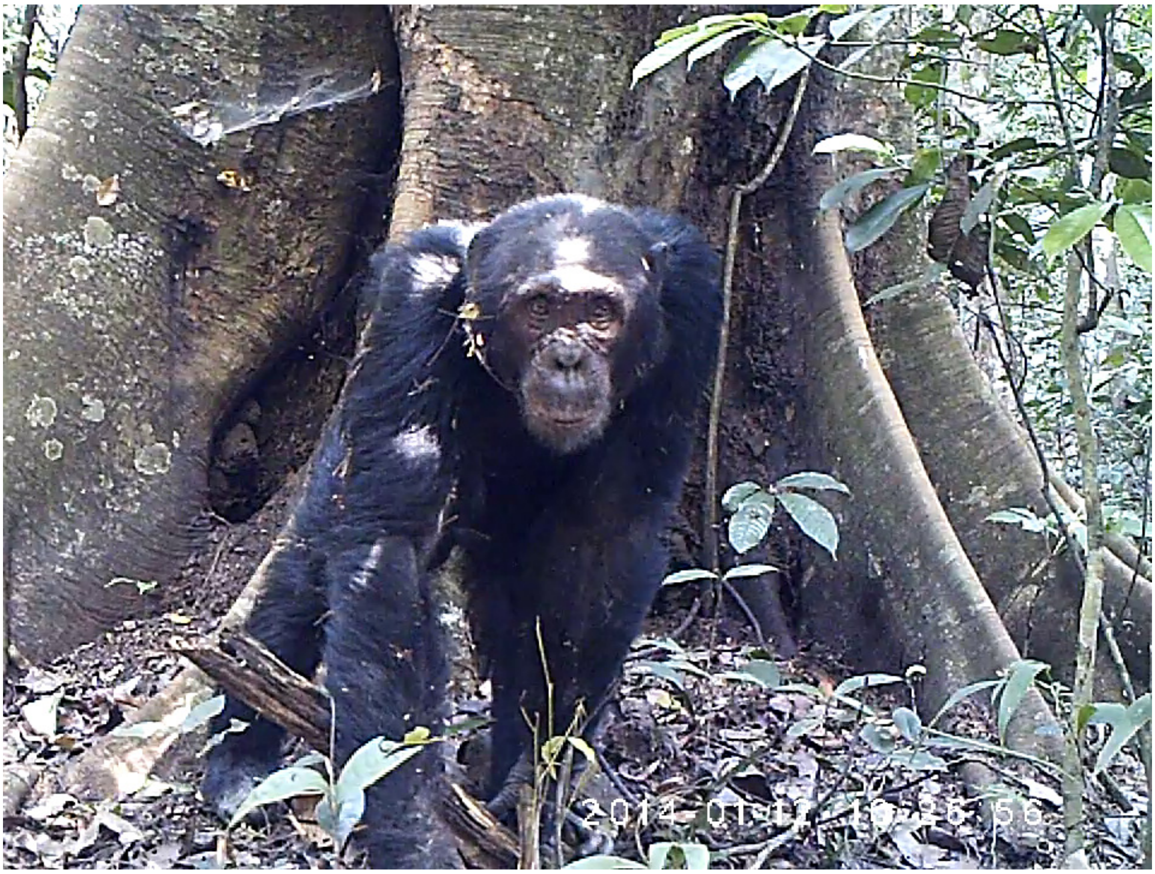


Fig. 04.01. Chimpanzee at Kwano study site in Gashaka Gumti National Park Nigeria. (Snapshot from video-camera trap, 12Jan14 © GPP)

INTRODUCTION

The ultimate demographic success of extant humans is largely based on our ability to adapt to varying ecological conditions – both in terms of different habitats and the seasonal constraints within them. Two highly adaptable primate taxa have traditionally been viewed as behavioural models for extinct hominins (Moore 1996): baboons and chimpanzees. Research of the current thesis explores a particular feature of these primates as a measure of their adaptability, i.e., how their basic pattern of gregariousness is influenced by the seasonal availability of food. For baboons inhabiting the Gashaka study site, this will be detailed in *Ch. 05* and *Ch. 06*, while the current *Ch. 04* will place emphasis on chimpanzees.

Chimpanzees have been studied across Africa since the 1960s, and extensively at some sites (reviews in Goodall 1986, Wrangham *et al.* 1994, Boesch & Boesch- Achermann 2000, Boesch *et al.* 2002, Reynolds 2005, Nishida 2011, Wilson 2012). However, very little is known about the rarest and genetically most distinct chimpanzee subspecies, the Nigeria-Cameroon chimpanzee (Morgan *et al.* 2011). Studies initiated by the *Gashaka Primate Project* (Sommer & Ross 2011) have started to fill this gap. Research described in this section continues this quest, compiling long-term data generated by a succession of field workers to better understand one of the most salient pattern of chimpanzee sociality: the dynamics of their fission-fusion social system.

It is well established that chimpanzees form communities which split into sub-units, so-called "parties" (see below for a definition of terms). While some investigators assume that food availability is the major influence on party sizes, others have proposed alternative factors (cf. review in Newton-Fisher *et al.* 2000). A list of variables propositioned to shape chimpanzee party size includes (i) the overall abundance of food (e.g., Basabose 2004), (ii) the spatial distribution of food in patches (e.g., Chapman *et al.* 1995), (iii) the number of cycling females displaying ano-genital swellings (e.g., Goodall 1986, Stanford et al. 1994), (iv) the seasonal formation of hunting parties that prey on monkeys (dry season at Gombe / Tanzania, Stanford *et al.* 1994; wet season at Taï / Ivory Coast, Boesch 1996). In reality, it will be extremely difficult to disentangle the causal effects of such a diverse portfolio – not least, because conclusions reached about particular influences are often based on relatively short study periods. However, given that food availability varies not only within a given year, but can also differ between years, there should be some caution to arrive at conclusions about what is "typical" for a given site.

The present chapter will employ records collected over more than a decade (2001–2014) at Gashaka about a basically non-habituated chimpanzee community that is nevertheless of extraordinary importance for our understanding of the socioecology of chimpanzees, given that they form a very extensive data set about the least known subspecies. The data will be used (i) to quantify the size of the community and the size of its territory, (ii) to compute the variation in the sizes – and to a degree composition – of day groups and night groups, (iii) to relate the variation in party sizes to the temporal and spatial availability of fruit as the staple food, i.e., their general abundance as well as distribution in patches.

The Nigeria-Cameroon Chimpanzee

Within the order of primates, chimpanzees (*Fig. 04.01*) belong to the superfamily Hominoidea. This taxon includes the "small apes" – gibbons and siamang (Family *Hylobatidae*), restricted to South Asia – and the "great apes" – the Asian taxon orangutan (*Pongo sp.*), as well as the African taxa gorilla (*Gorilla sp.*), chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), with humans (*Homo sapiens*) also being part of the African clade. Together with their *Pan*-cogener, bonobos, chimpanzees are the closest living relatives of humans, and might have shared a last common ancestor as recently as 4.3 million years ago (Gagneux 2004, Arnold 2008).

Chimpanzees have the widest geographical distribution of all apes due to their considerable ecological flexibility (Caldecott & Miles 2005). Still present in 21 African countries, they are thought to be extinct in Gambia, Benin, Burkina Faso, Togo, and Zambia. Four chimpanzee subspecies are identified nowadays (*Fig. 04.02*), denominated as East African, Central African, West African and Nigeria-Cameroon chimpanzee. The bonobo or pygmy chimpanzee is restricted to the southern banks of the Congo River and does not have subspecies. Chimpanzees might look slightly different according to subspecies, with West African forms sporting a thin fur and black face and Central African a paler face. East African chimpanzees are similar to the Central African variety, but with longer body hair. The Nigeria-Cameroon chimpanzee does not seem to possess distinguishing characteristics, and can show either black or pale faces.

Fig. 04.02. Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus):* Current vs. assumed historical (hatched) geographical distribution, plus location of important field research stations. Chimpanzee subspecies: *P. t. verus* (West African chimpanzee); *P. t. vellerosus* aka *ellioti* (Nigeria-Cameroon chimpanzee); *P. t. troglodytes* (Central African chimpanzee); *P. t. schweinfurthi* (East African chimpanzee). There are no subspecies for the bonobo or pygmy chimpanzee (*Pan paniscus*). (Map: © GPP / Maren Gumnior)

The overall geographical range of chimpanzees is estimated at 2,340,000 km^2 and believed to harbour between 152,000–255,000 wild chimpanzees. All subspecies are classified by the IUCN as at least endangered (Humle *et al.* 2016).

The Nigeria-Cameroon chimpanzee (*Pan troglodytes ellioti*, formerly *P. t. vellerosus;* Gonder *et al.* 1997, Kormos *et al.* 2003, Inskipp 2005) is restricted to terrain between the Sanaga River in Cameroon and rivers Niger and Benue in Nigeria (*Fig. 04.03*). Remnant populations west of the Niger may also belong to this subspecies and not to *P. t. verus*, perhaps indicating shifts of the bed of the river Niger as the presumed geographical barrier.

In Nigeria, the taxon occurs in Cross River NP and surroundings, including Afi Mountain Wildlife Sanctuary, and, as mentioned, in very small numbers in the south-eastern forests of the wider Niger delta, e.g., in Ise Forest Reserve (FR), Omo FR, Owo FR, Okomu FR and Okomu NP. However, the major stronghold of the species is Gashaka Gumti National Park and its vicinity (Adanu *et al.* 2011).

A regional action plan for the conservation of the subspecies (Morgan *et al.* 2011) estimates a population between 3,000–5,000 in Cameroon and 2,000–3,000 in Nigeria (Kormos *et al.* 2003; Ngalla *et al.* 2005, McManus 2005). However, figures may be much lower, with just about 3,600 individuals surviving, and 1,000 of these at GGNP (Sommer, pers. comm.).

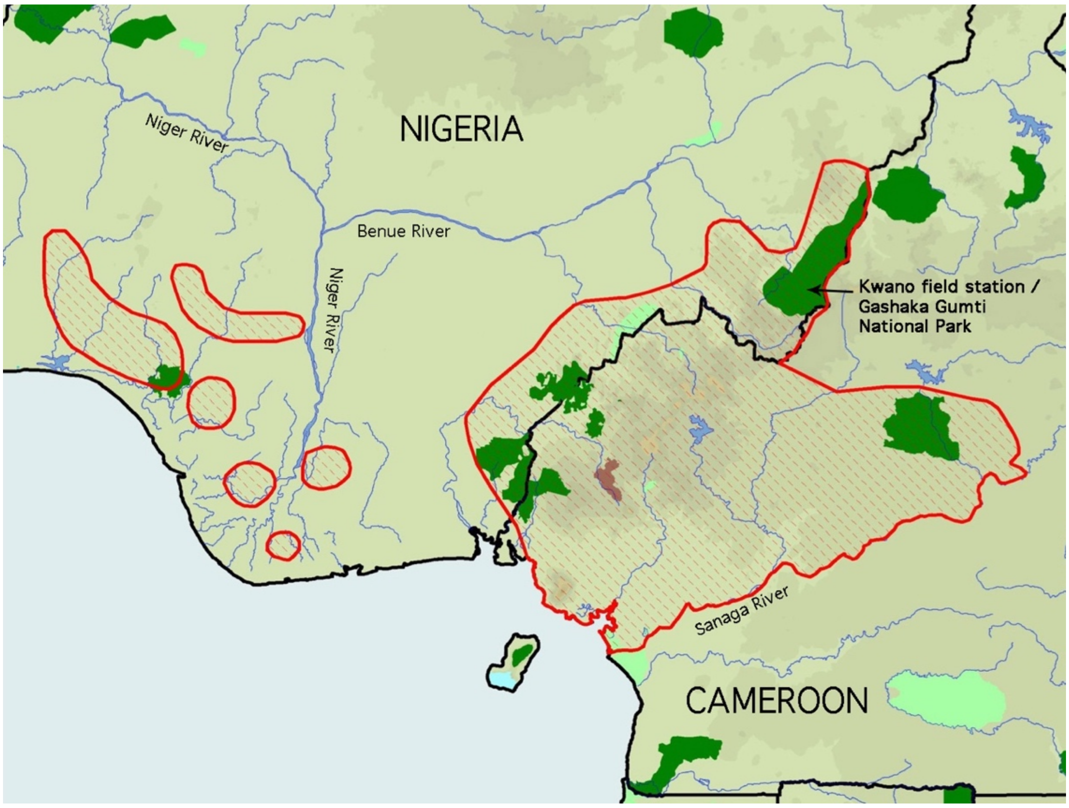


Fig. 04.03. Geographical distribution of Nigeria-Cameroon chimpanzee (red lines). Populations west of the Niger River are remnants with often only a few individuals left. (Changed after www.ellioti.org)

General Chimpanzee Socioecology

The literature on chimpanzee behaviour and ecology is vast, and a sophisticated review is beyond the scope of this thesis. However, basic features will be sketched out in the following to provide background information for the subsequent analyses that centre around how fruit distribution and seasonality at Gashaka-Kwano affects party sizes of the resident chimpanzee community.

Chimpanzees (for the following, see reviews in Boesch *et al.* 2002, McGrew 2004, Lonsdorf *et al.* 2010, as well as Pascual-Garrido 2011, co-researcher at Gashaka, from whom some of the following is adapted) are large-bodied primates, with average male weight 44 kg (range 37–60 kg) and that of females 36 kg (range 30–47 kg). Chimpanzees are agile arborealists, but can also knuckle-walk rapidly on the ground. They sometimes attain an upright position, for example, to reach a food source or during displays.

The basic reproductive parameters (see literature in Behringer *et al.* 2014) are as follows, with values indicating mean and range (r) of days (d) or years (y): (i) *menstrual cycle*: 32–36 d, with menstrual flow typically visible; around ovulation, females develop pinkish ano-genital swellings; (ii) *pregnancy*: 228 d (r 202–261 d); single infants, rarely twinning; (iii) *age of weaning*: 4 y; some infants may seek mothers' proximity until 10 y; (iv) *birth interval*: 4–6 y (r 2–8 y); (v) *age of first birth*: 13 y (r 11–20 y; r 5–32 y in captivity); (vi) *male sexual maturity*: 13–14 y; (vii) *mortality 1st year of life*: 22 % for males, 18 % for females; (viii) *life expectancy*: maximum 40 y (≥ 50 y in captivity).

Chimpanzees inhabit diverse biotopes such as evergreen and semi-deciduous rainforests, open woodland-savannah, gallery forests, and mosaic habitats that may include plantations and grassland. The apes form large multi-male / multi-female groups, so-called "communities" or "unit-groups" of between 20–100 members, which range over 5–38 km^2 in forests, and 25–560 km^2 in open habitats.

Each night – and at times during the day –, every group member (except dependent offspring) builds a new nest ("sleeping platform") from leafy twigs, typically in trees. The architecture of nests, location and size of nest groups and whether or not ground nests occur may be influenced by the risk of predation (reviews in Fruth & Hohmann 1996; Msindai 2018). Leopards are the main predators of chimpanzees. Lions can also pose a threat, though human hunters constitute by far the greatest danger.

Patchy distribution of food causes communities to break up and forage in smaller units, comprising typically about 6 members (range 3–10). Different individuals may join these units ("fusion") or split from them ("fission") (see review in Newton-Fisher *et al.* 2000). It is customary to denote diurnal units as "day parties" or "foraging parties" (although these sub-groups also rest and socialise together). Nocturnal units where individuals construct sleeping platforms in close proximity to each other are commonly termed "sleeping parties" (although they are not always sleeping) or "nest groups". To avoid semantic confusion with "nests" of insects, diurnal and nocturnal sub-units are labelled here as *day groups* and *night groups.* The groups communicate with each other via long-distance sounds, i.e. vocalisations (e.g., pant-hoots) and drumming, for which they typically beat with hands or feet on buttress roots.

Males are philopatric whereas females tend to leave their natal community upon sexual maturity. Males are generally closely related and cooperate to defend their range against neighbouring communities. Given these habits, home ranges are called "territories". Aggressive intergroup encounters are common and may go on for years until a neighbouring group is exterminated ("proto-warfare"; "lethal raiding"; Wrangham & Peterson 1996; Mitani *et al.* 2010).

Chimpanzee diet varies considerably across populations. Nevertheless, the *preferred food* is ripe fruit (56–71 % of foraging time), while *filler fallback food* is represented by leaves (18–21 %) as well as bark, terrestrial herbs and pith (11–23 %). Figs are the major *staple fallback food* (up to 91 %, according to Harrison & Marshall 2011), although their role is disputed, as figs are a preferred food at some sites (e.g., Dutton & Chapman 2014). The classification of animal matter is likewise a matter of debate. In any case, at some sites, vertebrates are preyed upon (0.3–6 %), comprising of at least 25 species (80 % colobus monkeys, 20 % mammals such as duikers, bush pigs, baboons and rodents), which may be hunted upon cooperatively. Occasional attacks on human infants by wild chimpanzees have also been registered, with victims being eaten at least partly (e.g., Goodall 1986, McLennan 2010). Cannibalism does likewise occur, with unrelated infants a favourite target. Moreover, in some habitats and to various degrees, chimpanzees exploit colonies of eusocial insects such as termites, ants and bees to consume imagos, brood or honey – often aided by tools (McGrew, 1992; Pruetz 2006; Sommer *et al.* 2016). Chimpanzees will sometimes ingest soil, in particular from termite mounds, as well as small stones, presumably to detoxify food or to aid digestion. Self-directed coprophagy has also been observed, perhaps to repopulate the gut flora.

Wild chimpanzees manufacture and / or use a variety of tools from materials such as bark, leaves, sticks and rocks, as sponges, wipes, probes, hooks, drills, missiles and toys, to extract resources (water, insect prey, honey, seeds) and in social contacts (sexual invitations, conflicts, play; McGrew 2004). Some communities of West African chimpanzees and Nigeria-Cameroon chimpanzees (Morgan & Abwe 2006) gain extra nutritional benefits from the use of hammers and anvils of stone or wood to crack hard-shelled nuts. In general, females do more extractive foraging to harvest localised food sources such as social insects, while males do more hunting, a sex-typical behavioural pattern that may be homologous to the division of labour documented for human hunter-gatherer societies.

Each chimpanzee community is characterised by a unique combination of social customs, tool-kits, communication, territorial aggression, war-like raiding, hunting strategies, and plant consumption for food and self-medication. This diversity indicates the importance of social transmission of behaviour, and has become a staple theorem of "cultural primatology" (Whiten *et al.* 1999).

Study Aims

In this chapter, the emphasis will be on a particular aspect of chimpanzee socioecology: How does the changing temporal availability and spatial distribution of food brought about by the seasonal climate (cf. *Ch. 03*) influence chimpanzee gregariousness at its most basic level, i.e., with respect to the numbers of chimpanzees that forage together (day groups) or sleep together (night groups) ?

MATERIAL AND METHODS

Chimpanzee "Parties" – Problems of Definition

Clear-cut definitions of what constitutes a "party", i.e., a sub-unit of a chimpanzee community, are difficult to construct. Often, the recorded size is simply the number of individuals "together in one place" identified by an observer (cf. Newton-Fisher *et al.* 2000). But, how spatially extended can a "place" be, to qualify for chimpanzees to be counted as "together"? Are five chimpanzees that forage together in touching distance a distinct party, or should two other chimpanzees each of which forages alone, let's say, 30 meters from the cluster of five, be included in the party count? Also, which temporal interval has to pass so that a new count can be considered an independent data point? Moreover, some studies consider all individuals present as constituting the size of a party, whereas others exclude infants from the count (cf. Basabose 2004).

These problems relate largely to the estimate of day parties, where animals are on the move through their home range. The computation of night parties is much more straightforward, as chimpanzee nests are stationary and observers can visit them when the apes have left. This allows for a careful checking of the surroundings so that no nests in the vicinity are missed. Still, there is the problem that nests that have been built at different times are mistakenly combined into one group, albeit that limitation is mitigated when considering only freshly built nests.

In any case, such intra-site problems are amplified if one attempts inter-site comparisons, because in reality, different methodologies are the norm (Basabose 2004). As a result, "precise definitions of party membership and of the criteria necessary to reduce temporal dependence between successive observations vary between observers and between studies" (Newton-Fisher *et al*. 2000: p. 616). It is for that reason, that inter-site comparisons will be attempted only sparingly in the following analyses of fission-fusion dynamics of the Gashaka-Kwano chimpanzees.

As explained above, the terms "foraging party" or "nest party" are ambiguous. For that reason, neutral expressions will be employed to describe chimpanzee associations, i.e., the terms *day group* (in lieu of "day party" or "foraging party") and *night group* (in lieu of "sleeping party" or "nest group").

The specific methodology of how counts were arrived at is explained in the following.

Surveys of Chimpanzee Day Groups

Field assistants and researchers recorded sightings of large mammals in the wider Kwano study area, including chimpanzees (*Fig. 04.04*), over a 9-yr period for a total of 17,487 h (cf. *Tab. 02.02*; *Fig. 02.12*). These surveys, initiated in the year 2000 (Fowler 2006), grew out of initial efforts to habituate the Kwano chimpanzees to human observers (Fowler & Sommer 2004). The surveys were also used to collect chimpanzee faecal samples as well as to locate sites where the apes had harvested social insects and honey with the help of tools, which they then normally abandoned (Fowler *et al.* 2011).

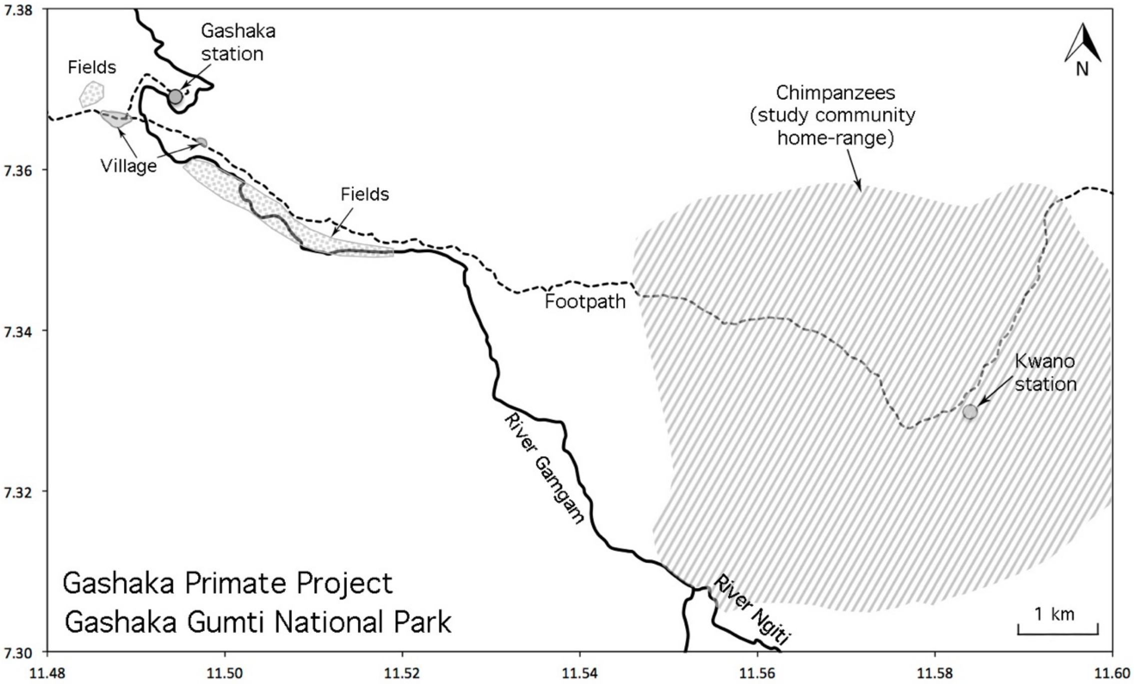


Fig. 04.04. Map with approximate extent of home-range of the Kwano chimpanzee study community and its location within the overall study area (cf. *Fig.02.03*). (Design: GJ)

Team members called these surveys "chimp patrols". The surveyors walked along established foot paths or specially cut trails or sat at elevated observation points such as rocky outcrops. They recorded time and location of vocalizations (pant-hoots, barks, screams) and the sound of chimpanzees drumming against buttress roots or tree boles. The number of persons in a given patrol – students, researchers, local field assistants, volunteers – could vary (1 = 19.6 %, 2 = 53.8 %, 3 = 18.1 %, 4 = 6.4 %, 5 = 1.2 %, 6 = 0.6 %, > 6 = 0.4 %; Sommer *et al.* 2004).

Whenever possible, patrols used auditory contact or recently constructed chimpanzee nests to make contact with the apes. Protocol included (i) not to approach further when chimpanzees were seen, (ii) not to hide upon visual contact but to make their approach known to the apes, e.g., by talking in a quiet voice, and (iii) to mock-chew vegetation once visible to the apes, to convey non-aggressive intentions. The Kwano chimpanzees would often tolerate human observers while at other times retreat more or less quickly. The patrols remained near the chimpanzees until they moved away. To follow the apes in the rugged terrain over extended distances was not normally possible. Surveyors would also meet chimpanzees by coincidence, usually near the footpath traversing the habitat. Information about these opportunistic encounters was included in the analysis.

Each sighting of chimpanzees was treated as an "encounter", defined as lasting from when the first chimpanzee was visible until the last disappeared. For encounters of only a few seconds, a minimum length of 1 min was used. At least 3 h had to pass before a new party count would enter into the analysis.

The maximum number of chimpanzees visible during an encounter was recorded, as well as their major activity and the group's age-sex class composition (adult male; adult female, with or without ano-genital swelling; adult of unknown sex; juvenile of either sex; infant of either sex). Movements in the vegetation, calls or drumming by non-visible individuals nearby indicated that more animals were present than the surveyors could count. In these cases, 1 additional individual was added to the number of visible animals. Infants were excluded from calculations of day group sizes (cf. Mitani *et al.* 2002), but juveniles more or less independent from their mothers were included.

Surveys of Chimpanzee Night Groups

Field assistants searched the Kwano terrain for chimpanzee nests and recorded number and location. These surveys covered two periods (2001–2009, 2012–2014), during both of which field assistants were instructed to locate all nests that constituted a night group (*Fig. 04.05*). The focus of the study periods was slightly different. During the first period, the interest was mainly on assessing night group sizes and also to collect faecal and hair samples from the nests. During the second period, research focused on nesting trees and whether these would be used repeatedly. As has been mentioned already, the problems of computing day nests related to the fleeting nature of encounters with unhabituated chimpanzees and inter-observer reliability are mitigated when counting night nests, as these are stationary.

Fig. 04.05. Forest at Kwano with an assemblage of nests built and used by chimpanzees during the previous night (20Apr10). (Photo: GJ)

Locations of Day Groups and Night Groups

From 2001–2009, surveyors did not collect GPS data, given a lack of suitable devices, but also limitations of technological literacy of the local field assistants. Instead, surveyors included information about the locale of chimpanzee sightings, acoustic signals and nest sites via permanent markers of footpaths and specially cut trails that criss-cross the habitat (cf. *Fig. 02.06*). These trails were fitted with permanent markers at intervals of 25 m. The GPS location of each marker was recorded at a later stage, and imported into Google Earth. The locale of nesting sites as recorded by the field assistants using trail markers was then transcribed into digital coordinates.

From 2012–2014, Garmin GPS units were used to obtain coordinates of nest groups, with data likewise imported into Google Earth.

Territory Size

As chimpanzees are notoriously territorial (Mitani 2010), it was assumed that all the sightings and nest locations were part of the study community's home range. For the estimation of territory size, the minimum convex polygon (MCP) method was used. MCP calculates home range size by drawing a convex polygon around location points (Boyle *et al*. 2009). Although MCP has limitations, especially its inability to distinguish between areas of high and low use, and also by incorporating areas within the polygon that might not be used (Pimley *et al*. 2005), it has been found to be the best home range estimation method for small sample sizes (Boyle *et al*. 2009).

Territory size was estimated by applying the MCP method to all data on chimpanzee sightings and nesting locations. Thus, the polygon encloses 100 % of recorded locations (similar to Newton-Fisher 2003), given that it seemed reasonable to include sightings outside the main sample area.

MCP were calculated via ArcView GIS version 3.2a with the Animal Movement Extension (Hooge and Eichenlaub 2000).

Fruit Availability

The seasonal availability of the chimpanzee staple food – tree fruits – was calculated via the number of fruiting trees and vines along an 8-km straight-line transect (see *Ch. 02*). A fruit-index was used based on the diameter at breast height (DBH) of fruiting trees. DBH is known to be a good predictor of fruit abundance (biomass) and has been widely employed in studies of primate feeding ecology (review in Newton-Fisher *et al.* 2000).

RESULTS

The chimpanzees of Gashaka Gumti National Park and the Kwano study site in particular are, till date, the best researched population of the least known subspecies, *Pan troglodytes ellioti* (*Fig. 04.06*).

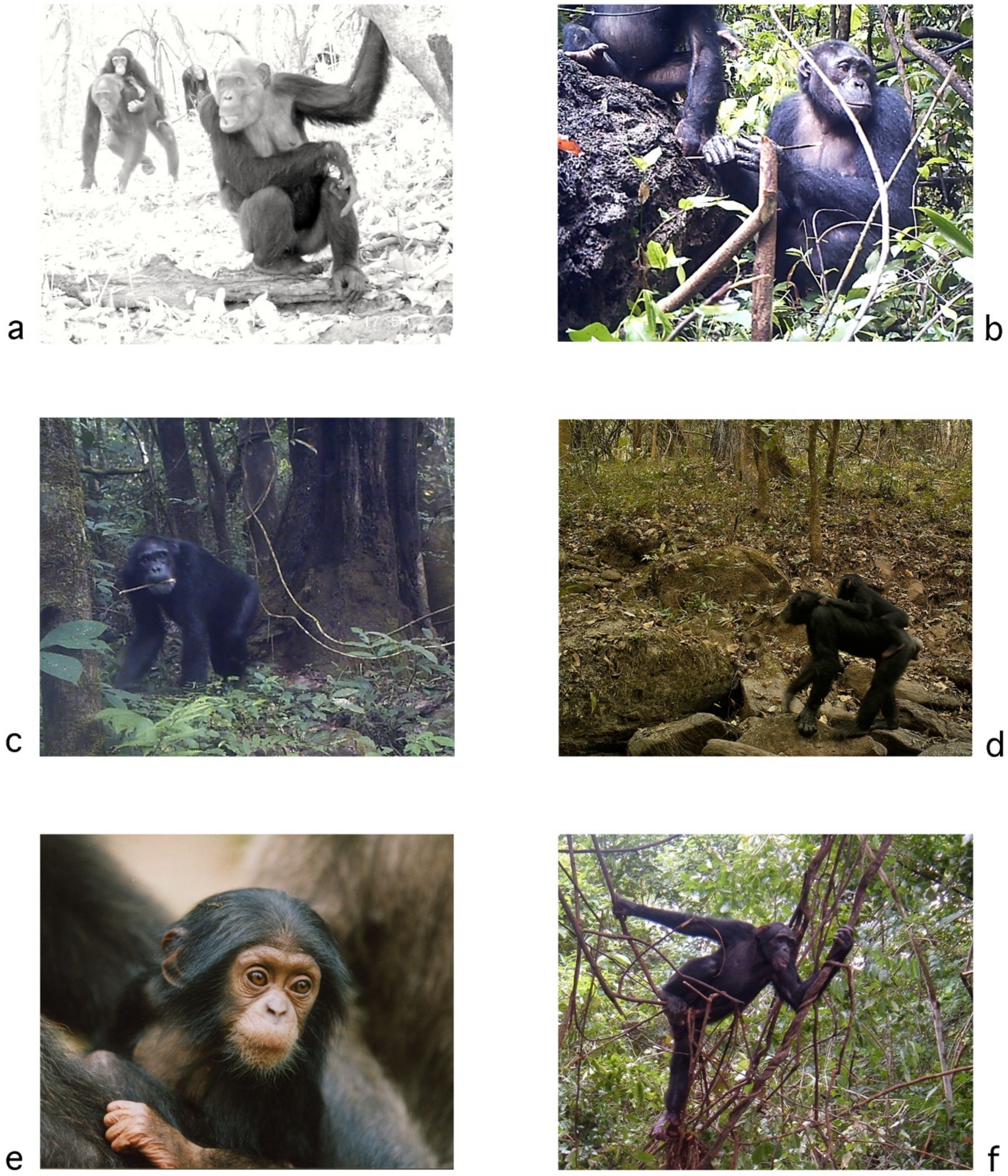


Fig. 04.06. Chimpanzees of Gashaka-Kwano. (a) Chimpanzees moving at dawn (2013). (b) Getting honey from stingless bee hives (2013). (c) Carrying a probing stick for honey collection (2013). (d) Mother with infant travelling in a river bed (2013). (e) Infant in Afi Mountains sanctuary near Gashaka Gumti National Park where some of the orphans produced by the bush meat trade end up (2005). (f) Chimpanzee caught in a hunter's snare at Mayo Kpaa, outside the study area; this is the only report of such incident in Gashaka Gumti National Park (2009). (Photos: © GPP, [a, b, c] video-camera traps, Anthony Agbor, [d] still-camera trap, Gonçalo Jesus, [e] Yvonne Pohlner, [f] National Park Service)

Territory Size

The likely extent of the Kwano community's territory was derived from plotting the locations of close to 200 sightings of day groups and locations of more than 300 nesting groups recorded over approximately 14 years (*Fig. 04.07*). This suggests that the apes use an area of 27.5 km^2. However, this figure should be treated as an estimate, as (i) the MCP method may include unused parts of the home range (Pimley *et al*. 2005), resp. (ii) the chimpanzees may have ventured into areas for which there are no observational records. Clustering of data does not necessarily reflect a bias in collection, because despite extensive forest surveys, certain sections of the wider study area were found to hardly ever harbour nesting sites. Instead, the chimpanzees seem to prefer certain places more than others, such as rather dense forest.

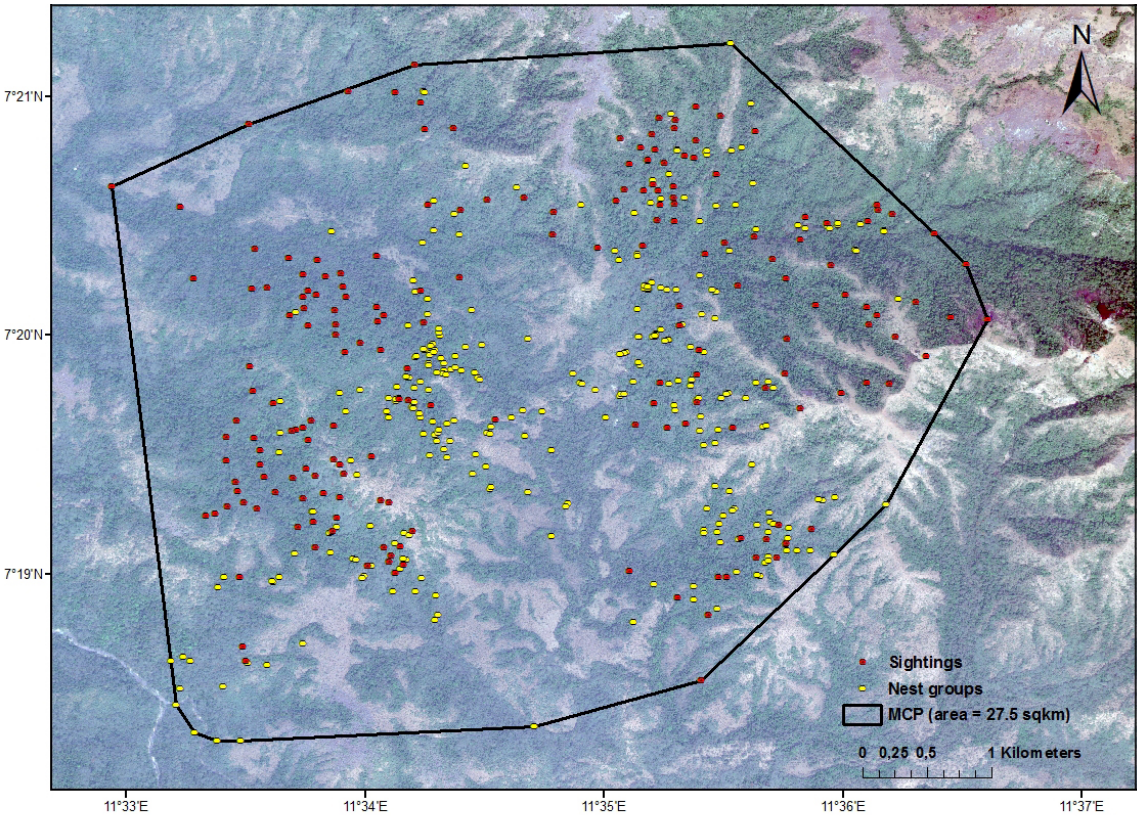


Fig. 04.07. Estimated territory use by the Kwano chimpanzee community. MCP = minimum convex polygon (100 %, area = 27.5 km^2). Red dots = locations of 189 sightings of chimpanzee day groups ("foraging parties"; 2000–2001, 2005–2008). Yellow dots = locations of 330 night groups ("nesting parties"; 1041 nest trees) (Jan 12–Aug 13). (Design: GJ)

It is assumed that the map indicates the rough extent of the Kwano community range, given certain geographical features. Thus, the northern and western sides of the territory are characterized by steeply ascending hills and cliffs. Beyond these spread deforested grassland resp. thinly treed woodland-savannah – rendering it likely, that these areas are not utilized by the chimpanzees (cf. *Fig. 04.04*). Towards the south, the territory approaches human settlements near Gashaka, which again reduced the likelihood of frequent visits. Although nests can be sometimes found around Gashaka, these may belong to a neighbouring community. Towards the south, the territory borders the banks of the river Ngiti and the river Gamgam. It is unlikely that chimpanzees, during the height of the rainy season (May–Oct), can cross the then torrential and wide Gamgam. Vocal exchanges between chimpanzees were heard several times across the banks of the Ngiti river. It is therefore assumed that another community ranges towards the south of the Ngiti / Gamgam confluence.

The size of the community is estimated to encompass about 35 members (see below).

Encounter Frequencies

As part of the extended large-mammal foot surveys at Kwano, chimpanzees were encountered during every month of the year. However, sightings are more prevalent from Mar–Jun, a consistent pattern over a 5-yr study period (*Fig. 04.08a*). Visual encounters are often facilitated by first hearing the apes, because they call or drum against wood. In fact, the likelihood to hear such sounds is tightly correlated with the frequency of sightings (*Fig. 04.08b*). A similar co-variation is apparent in the diurnal distribution of encounters (*Fig. 04.08c*). Thus, the chimpanzees tend to be noisier during the early morning and late afternoon. Peaks and reductions in diurnal sound records are tightly correlated with corresponding likelihoods to actually spot the apes.

Over the 5 years of systematic surveys for large mammals by field assistants and researchers, habituation of the chimpanzees progressed. This can be deduced from the fact that the duration of time observers spent near the apes – "seeing" them – increased significantly ($p = 0.006$), the longer these surveys were in effect (*Fig. 04.09a*). The length of encounters was also significantly ($p < 0.001$) influenced by the number of spotted animals, i.e. the larger the day group, the longer lasted the sightings (*Fig. 04.09b*).

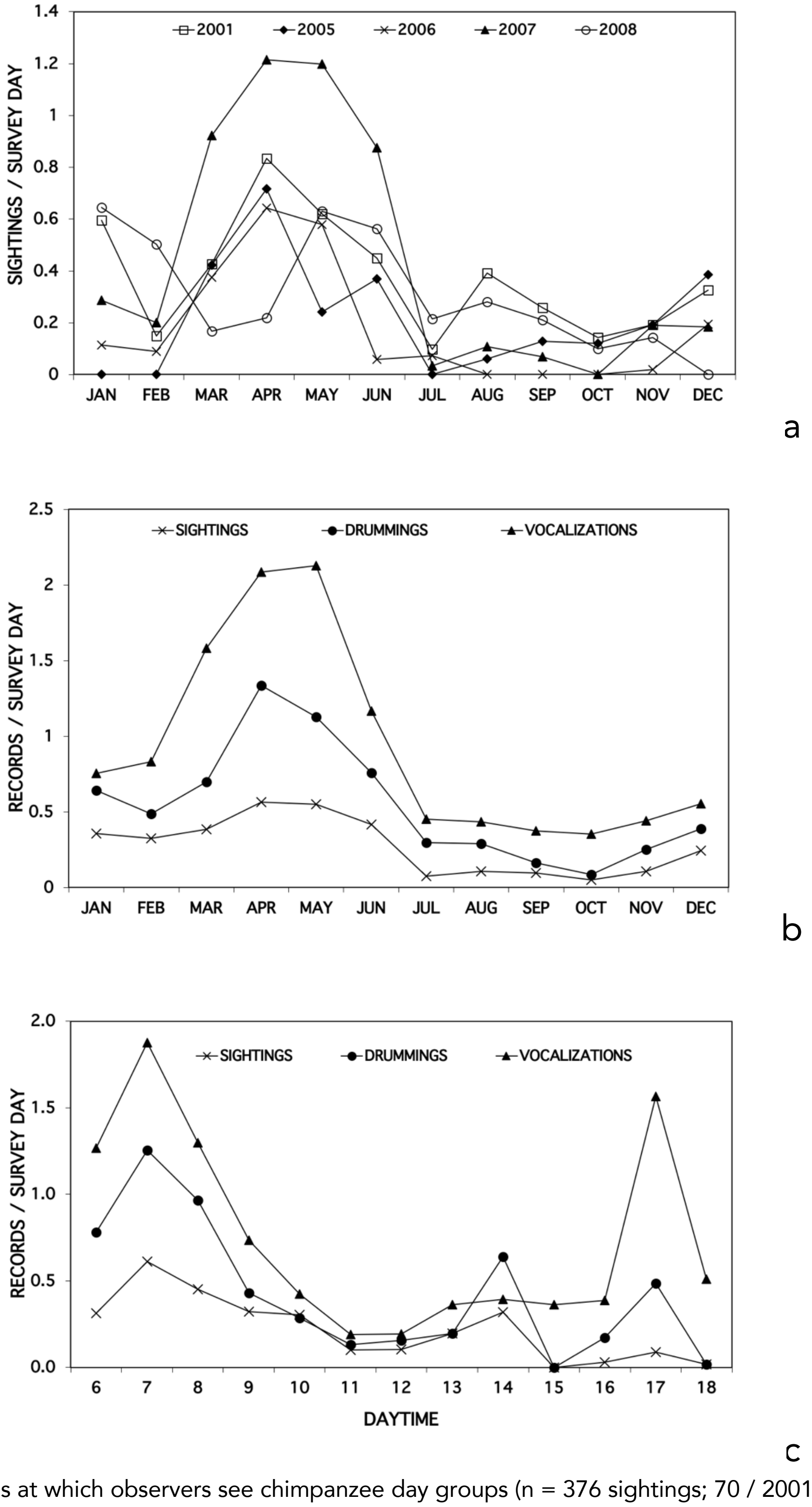
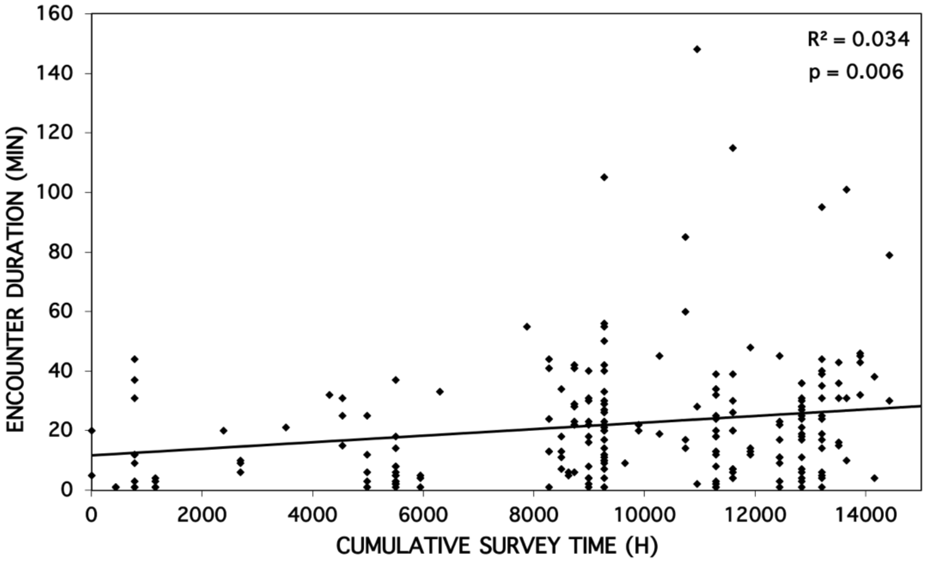
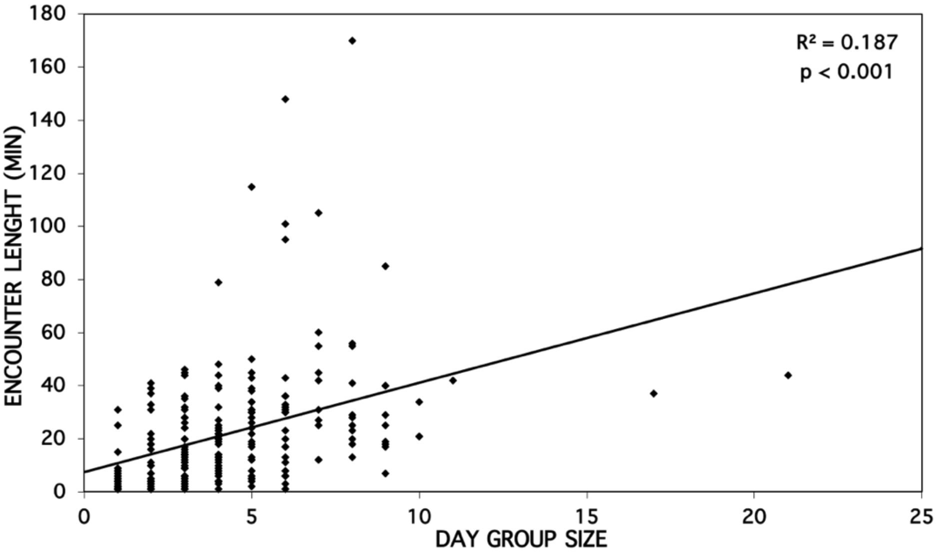


Fig. 04.08. Rates at which observers see chimpanzee day groups (n = 376 sightings; 70 / 2001; 76 / 2005; 68 / 2006; 69 / 2007; 93 / 2008) and hear drumming or vocalisations (2005–2008). Rates indicate encounter probability during a hypothetical cumulative survey day of 13 h (06:00–18:00). Based on foot surveys detailed in *Tab. 02.02.* (a) Monthly sightings during individual years. (b) Monthly sightings, drumming and vocalisations across all years. (c) Diurnal likelihood of seeing or hearing chimpanzees



a



b

Fig. 04.09. Duration of encounters (sightings) with chimpanzee day groups. Based on foot surveys detailed in *Tab. 02.02.* (a) As a function of cumulative survey time (Single linear regression: F(1,216) = 7.604, $p = 0.006$ **, $R^2 = 0.034$). (b) As a function of day group size (Single linear regression: F(1,215) = 49.54, $p < 0.001$ ***, $R^2 = 0.187$)

Day Groups

Reflecting their fission-fusion mode of sociality, chimpanzees of the about 35-member strong Kwano community split up into day groups of various sizes. Most commonly, chimpanzees are encountered as duos. However, day groups may be as large as 21 individuals (*Fig. 04.10*, *Tab. 04.01*). The average number of encountered apes fluctuates between 3.1 and 5.6 animals across the 6 individual study years – with an overall mean of 4.2 animals.

A factor influencing day group sizes is presence or absence of females with sexual swellings. Thus, groups that include fertile females average 5.1 animals, while those without only 3.6 animals. Previously this association had already been observed (Sommer et al. 2004) but most likely due to sample size, the statistical test was not significant ($p = 0.09$, data for 2000–2001), in this study however, it was possible to confirm such influence (Mann Whitney U-test: $n_{S-} = 254$, $n_{S+} = 106$, $p < 0.001$). Presence or absence of infants has a similar effect, in that groups are larger by 1.7 animals when an infant (or, rarely, more than one) is in their midst ($n_{I-} = 267$, $n_{I+} = 98$, $p < 0.001$) . This effect is not simply due to adding infants, as these are excluded from the counts.

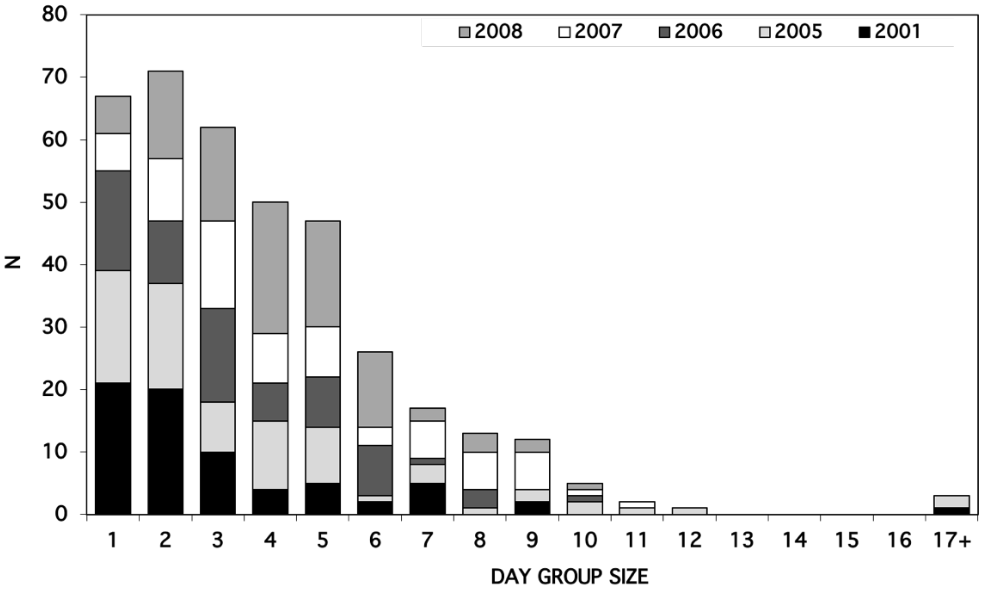


Fig. 04.10. Sizes of chimpanzee day groups. Based on foot surveys detailed in *Tab. 02.02*

Tab. 04.01. Size variables of chimpanzee day groups. Figures include an unknown number of double-counts of identical individuals. Based on foot surveys detailed in *Tab. 02.02*

Parameter	Day party size	Mean	Min	Max	SD	n
	2000–2001	3.7	1	17	3.5	95
	2005–2008	4.0	1	21	2.7	310
	Overall mean	3.9	1	21	3.1	405
Yearly mean						
	2000	5.6	1	16	4.6	25
	2001	3.1	1	17	3.1	70
	2005	3.9	1	21	3.6	76
	2006	3.4	1	10	2.2	68
	2007	4.7	1	11	2.7	69
	2008	4.2	1	10	1.9	93
	Overall	4.2	1	21	2.3	401
Females with swellings						
present	2000–2001	5.6	1	14	3.7	9
	2005–2008	4.7	1	10	2.1	97
	Overall mean	5.1	1	21	2.9	106
absent	2000–2001	3.5	1	17	3.4	86
	2005–2008	3.4	1	21	2.9	157
	Overall mean	3.5	1	21	3.2	243
Infants						
present	2000–2001	4.7	1	16	3.7	26
	2005–2008	5.1	2	17	2.7	72
	Overall mean	4.9	1	21	3.2	98
absent	2000–2001	3.4	1	17	3.1	69
	2005–2008	3.3	1	21	2.7	198
	Overall mean	3.4	1	21	2.9	267

As for the composition of day groups (*Tab. 04.02*), adults constitute 79 % of animals seen, 9 % are infants, with proportions of juveniles being slightly higher (12 %). The M / F sex ratio is fairly even (0.9), with slightly more females (53 %) than males (47 %).

The data were also mined for the composition of unisexual day groups. The largest proportions are either sole adult males (22 %) or duos of adult females (22 %), while duos of adult males are rarely observed (5 %). Lactating mothers (with dependent infants) constitute 36 % of all unisexual day groups, a likely underestimate, as mothers with infants are probably particularly wary of surveyors (Bertolani & Boesch 2007).

Moreover, averaged across all months, about one third (34 %) of females seen in day groups exhibit swellings (range 0.0–65 %).

Tab. 04.02. Composition variables of chimpanzee day groups. Based on foot surveys detailed in *Tab. 02.02*

Day group composition (a)	Adult	Juvenile	Infant	Sum
2000-2001	245	27	30	302
2005-2008	827	165	83	1075

	%	%	%
2000-2001	81.1	8.9	9.9
2005-2008	76.9	15.3	7.7
Mean	79.0	12.1	8.8

Operational sex ratio (b)	Adult male	Adult female	Ratio
2000-2001	43	48	0.9
2005-2008	176	195	0.9
Sum	219	243	462
%	47.4	52.6	

Unisexual day groups (c)	Year	n	% (a)
1 AM	2000-2001	18	
	2005-2008	5	22.1
2 AM	2000-2001	3	
	2005-2008	2	4.8
1 AF	2000-2001	13	
	2005-2008	2	14.4
1 AF + 1 I	2000-2001	7	
	2005-2008	6	12.5
1 AF + 1 J	2000-2001	0	
	2005-2008	1	1.0
1 AF + 1 I + 1 J	2000-2001	18	
	2005-2008	2	19.2
2 AF	2000-2001	18	
	2005-2008	5	22.1
2 AF + 1 I	2000-2001	0	
	2005-2008	1	1.0
2 AF + 1 I + 1 J	2000-2001	0	
	2005-2008	1	1.0
2 AF + 2 I + 1 J	2000-2001	1	
	2005-2008	0	1.0
3 AF + 2 I	2000-2001	1	
	2005-2008	0	1.0
		104	100.0

Proportion of estrous females	Year	Females	With swellings	%
Jan	2000-2001	10	3	
	2005-2008	23	7	30.3
Feb	2000-2001	2	1	
	2005-2008	15	6	41.2
Mar	2000-2001	4	0	
	2005-2008	24	6	21.4
Apr	2000-2001	4	1	
	2005-2008	38	8	21.4
May	2000-2001	3	0	
	2005-2008	49	34	65.4
Jun	2000-2001	9	1	
	2005-2008	36	17	40.0
Jul	2000-2001	2	0	
	2005-2008	6	2	25.0
Aug	2000-2001	3	0	
	2005-2008	7	3	30.0
Sep	2000-2001	2	0	
	2005-2008	7	5	55.6
Oct	2000-2001	0	0	
	2005-2008	2	0	0.0
Nov	2000-2001	2	0	
	2005-2008	9	4	36.4
Dec	2000-2001	6	2	
	2005-2008	10	5	43.8

(a) Only counts with known sex of all adults

(b) Adults 2005-2008 include 35 individual counts of "subadults"

(c) 2000-2001: 95 day groups; 2005-2008: 311 day groups

Further analyses related encounter frequencies as well as aspects of day group compositions to the availability of fruit. Thus, the likelihood that surveyors spot chimpanzees during certain months closely follows fruit abundance in trees and vines (*Fig. 04.11*; cf. *Fig. 04.08a, Fig. 04.08b*). This finding likely reflects a causal relationship, given a highly significant ($p < 0.001$) linear regression (*Fig. 04.12*). However, a significant correlation between monthly proportions of females with ano-genital swellings and fruit abundance was not found.

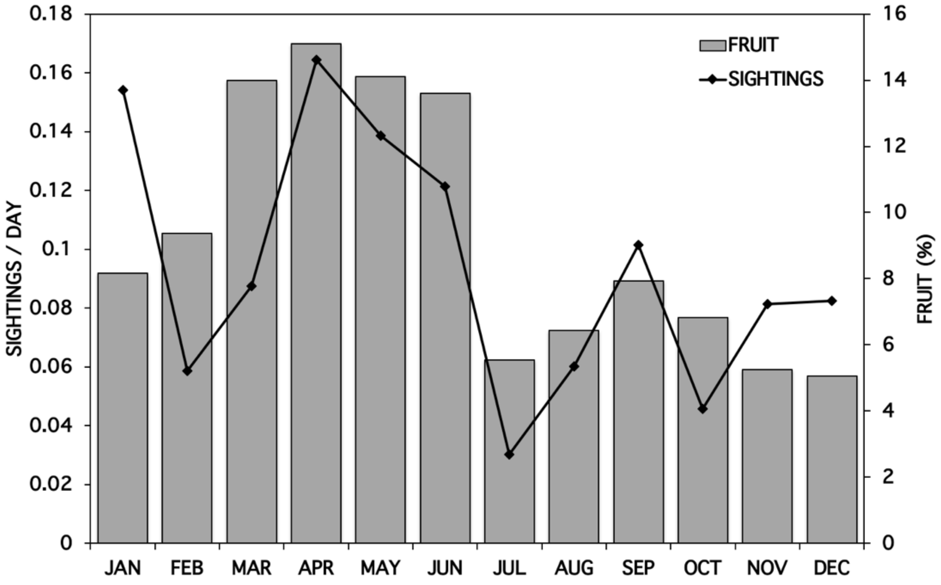


Fig. 04.11. Monthly sightings of chimpanzees in comparison with monthly percentage of fruit availability. Based on foot surveys detailed in *Tab. 02.02*

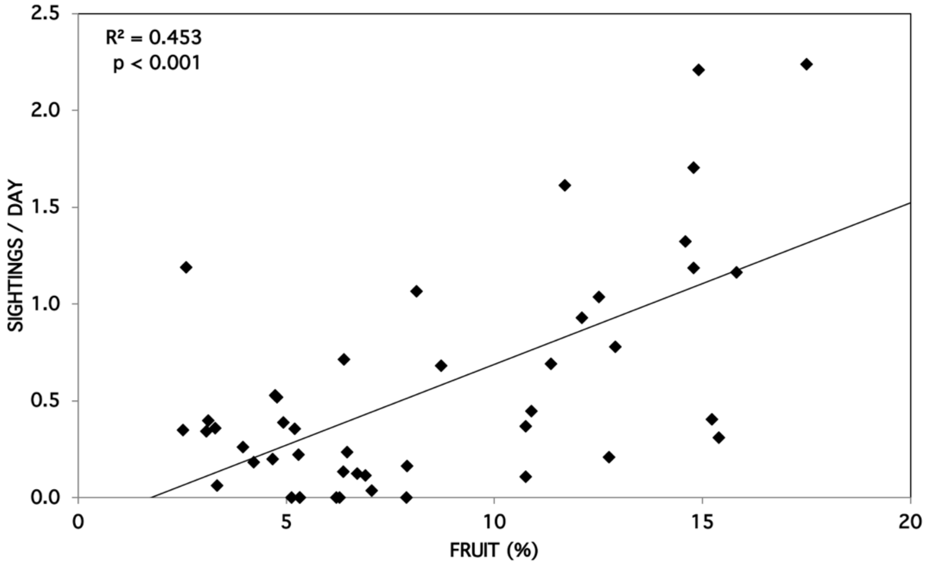


Fig. 04.12. Number of sightings per day as a function of monthly percentage of fruit availability (Single linear regression: $F(1,44) = 28.07$ $p < 0.001$, $R^2 = 0.389$). Based on foot surveys detailed in *Tab. 02.02*

Comparison of Day and Night Groups

The long-term data allow to compare the sizes of foraging and sleeping parties, and to elucidate potential causes of similarities or differences.

Average sizes of day groups do not fluctuate much between months, stochastic oscillations throughout individual years notwithstanding. Day groups are smaller than night groups during 9 out of 12 months (*Fig. 04.13*). Monthly sizes of night groups, however, display a striking seasonal pattern. They are considerably larger from Mar–Jun, with a marked decline thereafter (*Fig. 04.15*). This distribution was found independently for two survey periods (2001–2008, 2012–2014), despite slightly different methods of data collection there is a significant positive correlation ($p = 0.007$) between the two data sets (*Fig. 04.15*).

The seasonal variation in night group sizes coincides with the seasonal variation of fruit availability (*Fig. 04.16*). For both survey periods, means of monthly group sizes and habitat fruit production show a significant positive correlation (2001–2009: $p = 0.026$, 2012–2014: $p = 0.020$; *Fig. 04.17*).

The difference between day groups and night groups is most likely influenced by fruit availability as there is a significant linear regression ($p < 0.001$) for night group size as a function of fruit availability and no such relation is found for day group size (*Fig. 04.18*).

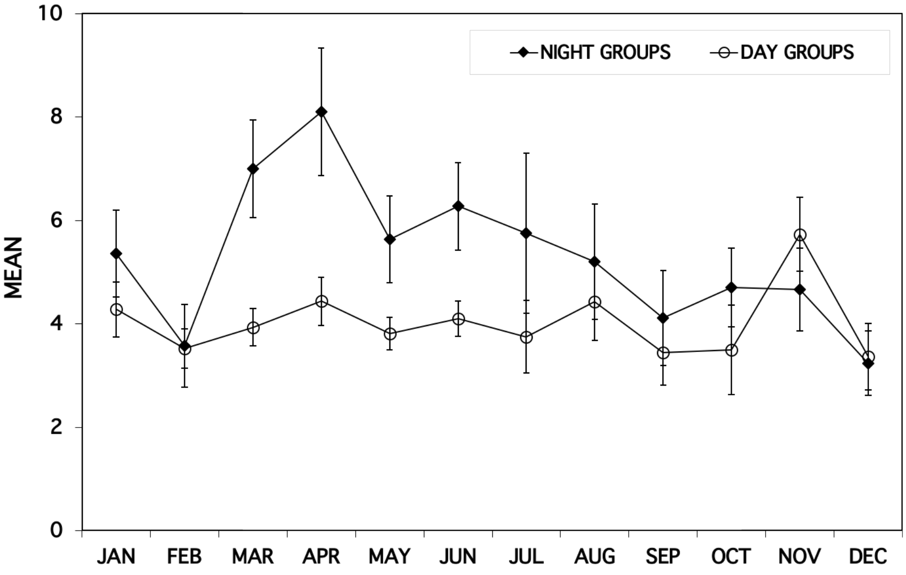


Fig. 04.13. Mean monthly sizes (± SE) of chimpanzee day groups (n = 306; 2001–2008) and night groups (n = 273; 2001–2008).

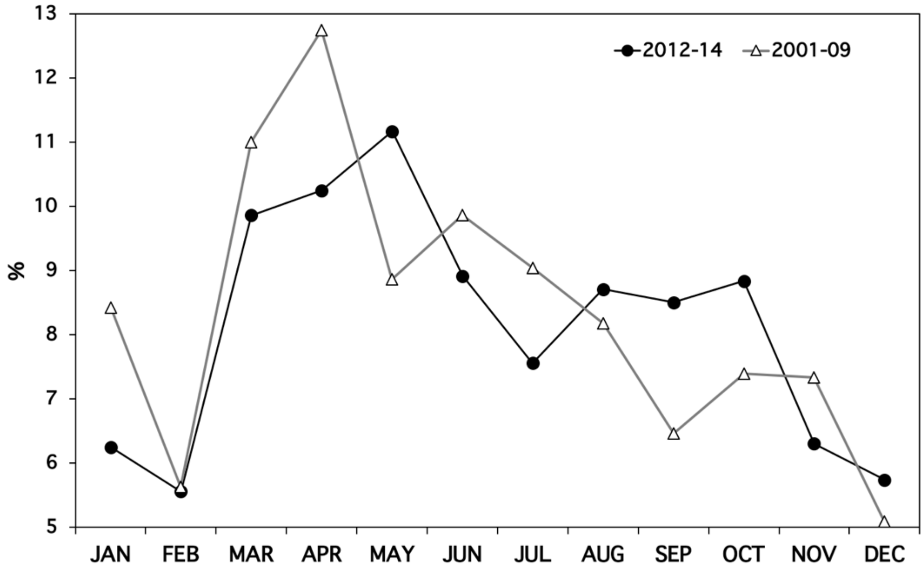


Fig. 04.14. Mean sizes of night groups. Data for 2001–2008 (n = 277 night groups determined via counts of fresh and new nests) compared to 2012–2014 (n = 592 night groups as determined from counts of nests of any age). Data transformed in % / month because of different counting methods

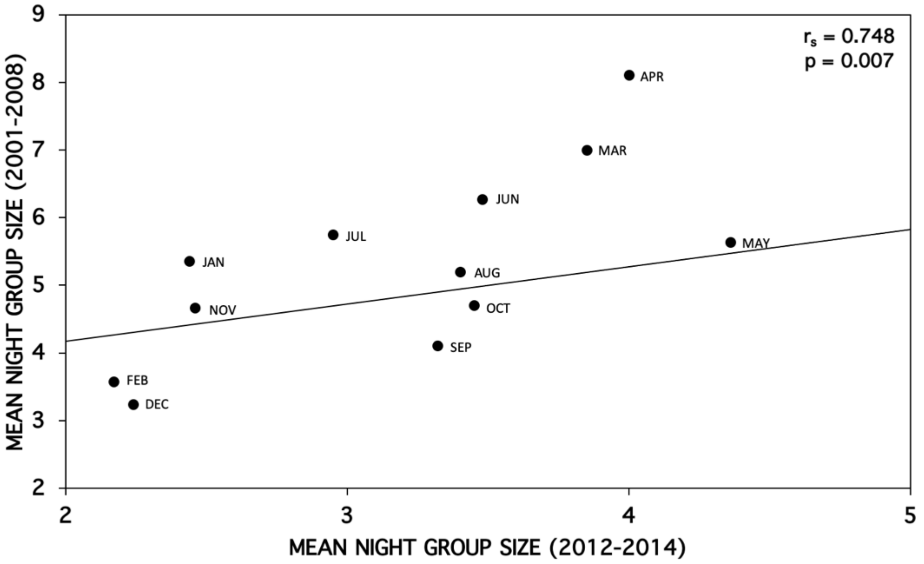


Fig. 04.15. Correlation between two different data sets of determining night group sizes (see *Fig. 04.14)* (Spearman's rank-order correlation: $r_s = 0.748$, p = 0.007**)

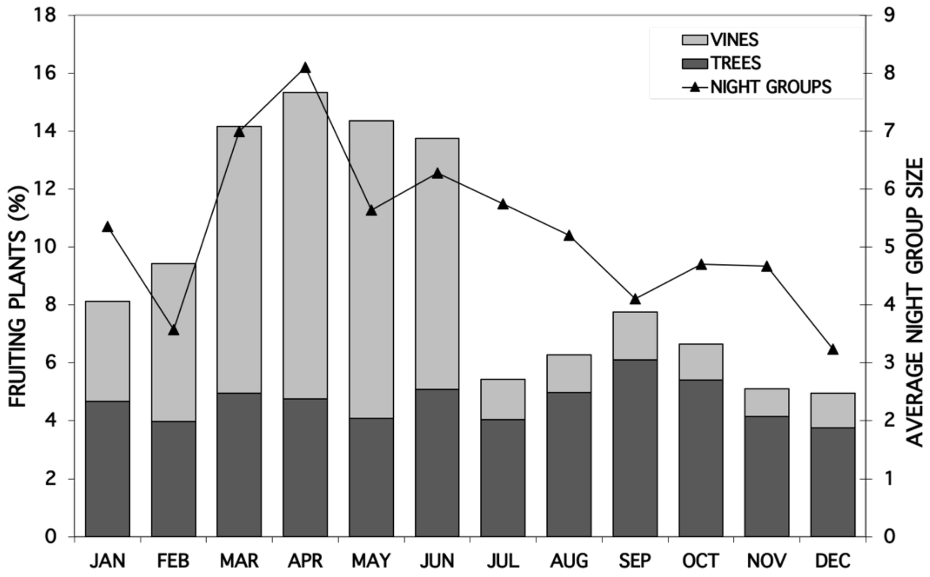


Fig. 04.16. Monthly sizes of chimpanzee night groups compared to the percentage of fruiting transect plants; combined data for 2001–2014. Based on 984 trees and 815 associated vines growing on a random 8 km straight line transect, monitored twice per month from Apr02–Jun09 (see Ch. 03)

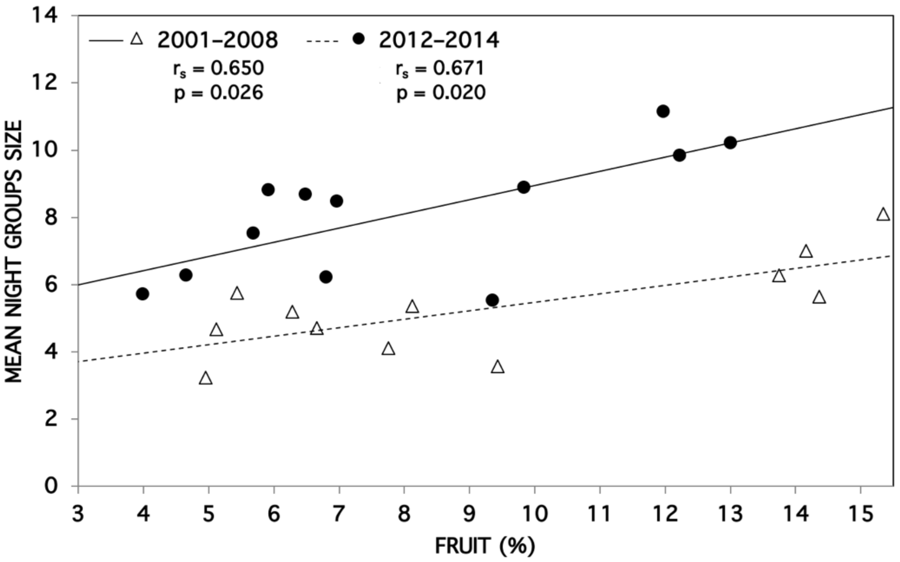


Fig. 04.17. Correlations of the average monthly night group and the percentage of fruiting transect plants. (Spearman's rank-order correlation: Years 2001–2009 r_s = 0.650, p = 0.026* Years 2012–2014 r_s = 0.671, p = 0.020*)

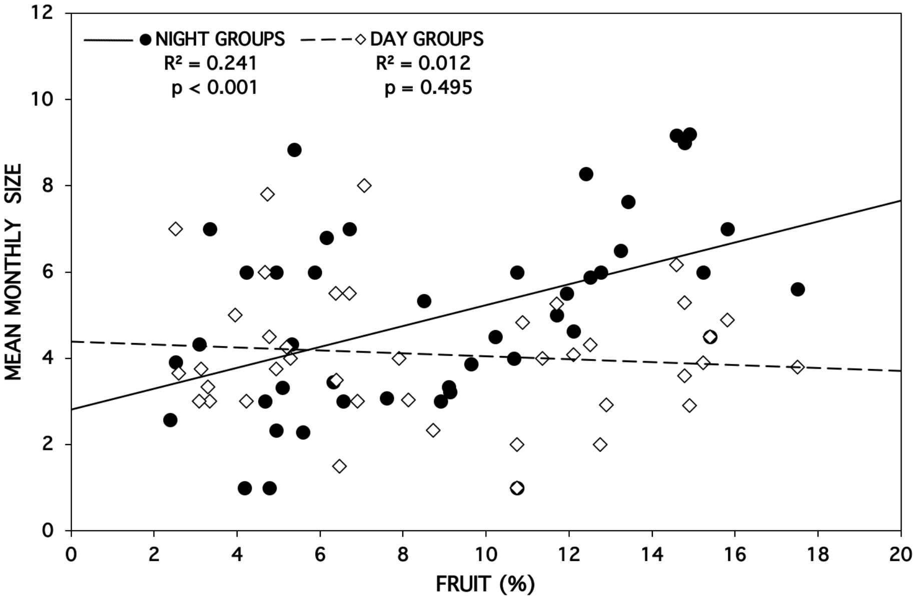


Fig. 04.18. Mean monthly night group (44 months) and day group sizes (40 months) as a function of monthly percentage of fruit availability (Single linear regression: Night groups F(1,42) = 13.31 $p < 0.001$ $R^2 = 0.241$, Day groups F(1,38) = 0.47 $p = 0.495$ $R^2 = 0.012$).

Community Size

The maximum number of chimpanzees recorded on a single day was on 27Jan01, when a group of schoolchildren and field assistants walking along an eastern trail spotted 17 apes who curiously watched the humans from the ground and trees over a period of 95 minutes. Two other nearby patrol teams heard or saw three other day groups estimated to comprise 4, 10 and 4 apes, thus bringing the total to 35 animals (Sommer *et al.* 2004). The largest nest group ever counted was 23 (Jul01). Given that about 20 % of the study population are infants or juveniles who sleep with their mothers (cf. *Tab. 04.02*), one arrives at a size of 28 for this nesting party. Assuming that some members slept elsewhere, this supports the assumption of a (minimum) community size of about 35. As chimpanzees were sighted across 27.5 km^2, population density was calculated as 1.3 apes / km^2.

DISCUSSION

Factors influencing ranging pattern and fission-fusion dynamics of chimpanzees (e.g., Newton-Fisher *et al.* 2000) living at Kwano compared to other study sites were discussed in the initial publication about this community (Sommer *et al.* 2004; see also Fowler 2006). However, sample sizes of that previous research were often small, derived from only 2 consecutive years of observations (2000–2001). The current study includes 4 additional years (2005–2008) of day group surveys, while data on nest groups are even more extensive (2001–2009, 2012–2014). The combined long-term data, bracketing 15 years, are hence much more comprehensive. The subsequent discussion, while following the general rationale outlined in Sommer *et al.* 2004, thus aims to confirm or revise previous explanations. Main focus will be on how the seasonal availability of fruit (abundance and distribution) influences the dynamics of the chimpanzee fission-fusion society, i.e. variations in the sizes (and composition) of day groups and night groups.

Surveying the Kwano Chimpanzee Community

Chimpanzees were heard or seen and nests were found in about 27.5 km^2 around the Kwano field station, as calculated via a MCP (cf. *Fig. 04.07*). Steep and barren hillsides leading into open grassland to the west and north, the proximity of Gashaka village in the east, as well as the relatively broad Gamgam river in the south-east seem to represent geographical barriers. Vocal exchanges between chimpanzees were heard several times across the banks of the Ngiti river. Thus, the Kwano area is likely to represent the core of what is believed to be a single chimpanzee community, including (a minimum of) 35 members.

At sites where chimpanzees are not habituated to observers, the easiest way to locate them is via acoustic signals. Chimpanzees vocally express emotions and convey information, e.g., about food sources and danger. Loud calls, particularly pant-hoots, are often given in the early hours of the day and again before nesting (Goodall 1986, Hunt & McGrew 2002). The most prominent non-vocal sound signal is drumming. In fact, the word for chimpanzee in Hausa, the prevalent local language around GGNP, is "biri mai ganga" (Nyanganji *et al.* 2011). In literal translation, this means "monkey with the drum", alluding to the long-distance sounds that chimpanzees produce when beating buttressed tree trunks with hands or feet.

From Mar–Jun, annual rates of sightings and sound records markedly increased (cf. *Fig. 04.08* *a, b*). A major cause is surely higher availability of fruit, particularly the peak in fruit production driven by vines (cf. *Tab. 03.10, Fig. 03.17*), which provokes chimpanzees to be noisy when entering large food patches and when forming nesting groups (see below; Notman & Rendall 2005). However, physical effects of climate also need to be considered. First rains may occur in March, announcing the end of the dry season, while April already sees an average of 211 mm (cf. *Tab. 03.03*). Once the forest floor starts getting damp, it is easier for surveyors to proceed quietly, without alerting the apes from afar through rustling and crackling dried leaves and woods. Similarly, ambient air will absorb less sound when temperature drops, which increases the likelihood that surveyors hear the chimpanzees. However, during the height of the rainy season, less acoustic signals and sightings were recorded –perhaps because foliage has now grown particularly dense, with water constantly dripping from leaves. These effects reduce visibility and muffle chimpanzee-produced sounds. Consequently, one expects sightings and sound records to pick up from when the rains stop. But, this effect is rather small, suggesting that some other factor might be at work.

Sounds such as drumming and pant-hoots that carry over considerable distances are typically produced by male chimpanzees (Clark & Wrangham 1994, Arcadi *et al.* 2004) and facilitate the fusion-fission dynamics (Fedurek *et al.* 2014). Such acoustics signals were more common during the early morning and late afternoon, when chimpanzees left their previous nesting sites or settled for a new one (cf. *Fig. 04.08c*). This finding is in line with the idea that smaller day groups join in the evenings to sleep in close proximity, to then split again in the mornings into smaller foraging groups (see below).

While sound records increase towards the evening, sightings do not. This is due to the fact that surveyors find it difficult to reach the locations from where the sounds originate as nightfall sets in. Moreover, surveyors were reluctant to scare the chimpanzees while they were building nests, and would rather use the sounds as cues to locate the apes the following morning.

Chimpanzees were generally wary, albeit at times curious, when surveyors approached them. Day group size was a good predictor of how long surveyors spent in visual contact with the apes (cf. *Fig. 04.09b*). If they were in larger groups, the principle of "safety in numbers" seemed to lead the ape to be more relaxed. A similar positive correlation between party size and the duration of observation was established at Kahuzi / DRC, "suggesting that chimpanzees tended to tolerate the presence of human observers best when in large parties" (Basabose 2004: 214).

When the *Gashaka Primate Project* was initiated in the year 2000, it was hypothesized that encounter rates and time spent with the apes would steadily increase. While this effect was found (cf. *Fig. 04.09a*), it was rather minimal and not enough to achieve habituation. Overall, direct encounters between observers and chimpanzees were not very frequent (n = 406, in 6 years).

Several factors contributed to the fact that habituation was never achieved. Firstly, the terrain at Kwano is often very steep and full of dense vegetation, which prevents researchers to follow the apes once they have been found. Secondly, various anthropogenic activities lead the chimpanzees to mistrust humans. These include poaching – albeit levels are low in the Kwano area – and people criss-crossing the terrain while moving between human settlements inside and outside the park (cf. *Fig. 04.04*). Thirdly, the *Gashaka Primate Project* relied heavily on local field assistants for the habituation efforts. However, experience from other ape-research sites (Volker Sommer, pers. comm.) nourishes the assumption that local field assistants, while often very dedicated, will not pursue habituation efforts in the same way, as ex-pat volunteers or researchers. Locals are, after all, a paid work-force, without the intrinsic motivation to want to conduct research on apes. Thus, virtually all successful ape-habituations elsewhere were led by ex-pats. In any case, chimpanzee research at Kwano quickly focussed on the collection of indirect data, often related to nest-building, tool-use and insectivory (Fowler 2006, Pascual-Garrido 2011).

Sizes of Day Groups

Day group sizes recorded for the Kwano community rarely exceeded 10 and were generally small, with a mean of 3.9 individuals (calculated by averaging the 2000–2001 figure of 3.7 and the 2005–2008 figure of 4.0; cf. *Fig. 04.10*, *Tab. 04.01*).

It is commonly assumed that the smaller the community, the larger the relative party size (i.e., mean party size/community size × 100; Boesch & Boesch-Achermann, 2000). If a size of 35 is assumed for the Gashaka-Kwano community, a day group size of 3.9 represents 11 % – a value close to, e.g., Budongo / Uganda (12 %, Wallis 2002) or Taï / Ivory Coast (13 %, Boesch & Boesch-Achermann 2000). Thus, the Gashaka data seems to confirm that smaller communities are socially less fluid, indicating that not only food competition influences fission-fusion (see below), but perhaps also predation pressure – exerted by leopards (cf. *Ch. 02*), human hunters – and threats posed by males from neighbouring communities.

Still, average day group sizes of under four individuals indicate that the semi-deciduous forest-savannah mosaic habitat seems to constrain the size of foraging parties. The most likely cause is the need to reduce feeding competition in what has been characterised as a "low-quality habitat" (Hohmann *et al.* 2006), given that many plants contain sub-optimal levels of macro-nutrients and relatively high levels of anti-feedants (Sommer *et al.* 2011). Moreover, tree patches at Kwano are small (mean DBH 24.3 cm) compared to evergreen rain forests at, e.g., Kibale / Uganda (mean DBH 68.4 cm for Kanyawara, mean 63.4 cm for Ngogo site). Consequently, compared to Kwano, foraging party sizes are double as large at Kibale (mean 8.4 at Kanywara, 7.3 at Ngogo; Potts *et al.* 2011).

The largest proportion of unisexual day groups (36 %) was constituted by lactating mothers (with dependent infants; cf. *Tab. 04.01*). This reflects findings at other sites, where mothers spent much or most of their time with only their dependent infants (review in Wilson 2012). In addition, it was found that sizes of mixed day groups increased when infants were present (cf. *Tab. 04.01*). This may be caused by nulliparous females being attracted to infants.

Another variable correlating with increased sizes of mixed day groups was the presence of females with swellings (cf. *Tab. 04.01*). It is well established from research at other sites that more males are present in parties that contain more cycling, swollen females (e.g., Emery Thompson & Wrangham 2006). However, the mechanisms for the formation of these larger subgroups are not clear. It may be that adult males are attracted to fertile females (Nishida 1983, Mitani & Watts 1997), or alternatively that tumescent females become more social because they seek out males to consort with them (Wilson 2012). Yet another possibility is that the initiative may come from males who join such groupings because their primary interest are interactions with other males (Newton-Fisher 2014).

Ripe fruit is the most commonly eaten and, actually, preferred chimpanzee food (e.g., Goodall 1986, Malenky *et al.* 1993). Thus, chimpanzees should adjust their behaviour in relation to fruit abundance. While foraging during lean times is a rather quiet affair – presumably to not attract competitors –, males in particular are known to produce loud, food-related vocalizations when finding and entering rich patches (Fedurek & Slocombe 2013, Schel *et al.* 2013). At Kwano, fruit production of trees and associated vines is markedly seasonal and peaks between Mar–Jun (cf. *Fig. 03.18*). This is, indeed, the same period when chimpanzees are heard most often, which, in turn, leads to surveyors spotting them with higher rates (cf. Fig. 04.08, *Fig. 04.11*, *Fig. 04.12*).

Primate female reproduction will often echo food availability, in that either conception or age of weaning correlates with high abundance (e.g., Indian langur monkeys; Borries 1999). While there is no evidence that wild chimpanzees give birth during certain times of the year, seasonal peaks in sexual receptivity have been reported (e.g., Tai forest: Boesch & Boesch-Acherman 2000; Mahale: Matsumoto-Oda *et al.* 1998; Gombe: Wallis 1997). Nevertheless, at Kwano, no correlation was found between the percentage of females with ano-genital swellings and fruit availability.

Asynchrony Between Sizes of Day versus Night Groups

Other things being equal, one would expect that day group sizes, i.e. the number of animals foraging together, are larger when more fruit is available. Surprisingly, this is not the case, as day group sizes were virtually constant throughout the year, thus not showing any association with general fruit abundance. Similarly, at Budongo / Uganda, food availability and day party sizes were not positively correlated (Newton-Fisher *et al.* 2000). This is in stark contrast to night groups, which do increase with increased fruit abundance (cf. *Fig. 04.16 – Fig. 04.18*). Such asynchrony between day and night group sizes (cf. *Fig. 04.13*) seems puzzling at first. However, these dynamics are probably caused by foraging constraints, as illustrated by a graphical visualization of the temporal and spatial distribution of fruit patches along the botanical transect (cf. *Fig. 03.20*). Thus, food patches do rarely occur in large clusters with many trees and vines fruiting in close proximity. Instead, fruit-bearing plants are spaced out across the habitat, i.e., it can typically be found in discrete single trees or vines, and only seldom in small groves of interconnected plants (Van Schaik & Brockman 2005). As a consequence, food competition is generally reduced in times of plenty, if one considers the whole habitat, but not for a particular food patch. This, it seems, forces the Kwano chimpanzees to continue to forage in small parties. For Budongo / Uganda, a similar conclusion was reached: "While the size of a patch limited the number of individuals that could feed together, the number of such patches increased as food became more abundant.

Consequently, chimpanzees did not form larger parties as food abundance increased, but instead made use of more food patches" (Newton-Fisher *et al.* 2000: 625).

The logic of this constraint can well be squared with the observation that chimpanzees form larger night groups during peaks of fruit availability. This is, because more individual food patches exist, which means that distances between them are reduced, and various chimpanzee parties can forage in relative proximity. Therefore, given reduced travel costs, chimpanzee day groups can merge more easily when nightfall is approaching, compared to periods when patches are more spaced-out.

An associated issue not touched upon in this thesis relates to the mental mechanism of how primates such as chimpanzees actually find their food. Numerous studies have taken the stance that animals do not simply crisscross their ranges in search of this food. Instead, they are believed to rely on memory about the distribution of patches (Garber 2000, van Schaik & Brockman 2005). We are still far away from understanding if and how such knowledge is updated, given the tremendous annual, supra-annual and sub-annual variability of phenophases (cf. *Ch. 02*).

CHAPTER 05

BABOON BEHAVIOUR.

ACTIVITY BUDGETS AND HOME RANGE USE

Fig. 05.01. Olive baboons of the wild-feeding Kwano troop engaged in grooming. (Photo: Alejandra Pascual-Garrido, 07Aug04 © GPP)

INTRODUCTION

The original socioecological model (Crook & Gartland 1966) aimed to disentangle if and how environmental factors influence, constrain and shape primate social structure (cf. *Ch. 01*). Numerous refinements – including refutations – were developed over the years, to accommodate our increased knowledge about inter- and intra-specific variability of behaviour (e.g., Foley & Standen 1989, Thierry 2007, Strier *et al.* 2014), a primate-typical trait that renders any deterministic approach problematic.

However, while primate researchers have recognised the importance of annual seasonal variation for some time, there is a growing recognition of supra-annual differences in terms of climate and plant phenology with resulting opportunities and constraints of diet acquisition (Alberts *et al*. 2005, Chapman *et al*. 2017).

The ability to cope with different environmental conditions – including anthropogenically altered habitats – via behavioural plasticity is particularly evident in the baboon clade (Barton *et al.* 1992). Still, while these monkeys have been extensively studied in open and relatively dry habitats, there is little information about baboons that dwell at the edge of their geographical distribution or those that inhabit a more forested, as opposed to open, environment which sees considerably rainfall.

The current research provides such information, by focussing on the behavioural ecology of baboons residing in a mixed forest-savannah subjected to a severe rainy season in Nigeria's Gashaka Gumti National Park. Baboons are a common sight at GGNP, from the surrounding buffer zone up to the 2500-m peak of Mount Gangirwal (Sommer, pers. comm.). When the *Gashaka Primate Project* was launched in the year 2000, Ymke Warren established two study troops which live 11 km apart from each other (Warren 2003) – one a crop-raiding troop near the village of Gashaka, the other exclusively feeding on wild plants and roaming around the Kwano field station (cf. *Fig. 02.03*). These were ultimately fully habituated to human observers and have been the subject of numerous specific investigations (e.g., Higham *et al.* 2009, Warren *et al.* 2011, Ross *et al.* 2011, MacLarnon *et al.* 2015, Sommer *et al.* 2016; see also *Appendix I*).

The following chapter investigates how baboons allocate space and time in relation to seasonal changes in their environment, by analysing patterns of home range use and activity budgets via the compilation and analyses of long-term records. None of these data have been previously published. Fractions of the information has informed results obtained during short-term studies. However, no previous work of baboon ranging and time budgeting at Gashaka (Warren 2003, Higham 2006, Ey & Fisher 2011, Alberts 2012, Thompson 2012) covered even a complete full calendar year, with the problem being that short-term studies may reach conclusions that turn out to reflect only a snapshot of environmental conditions once applicable longitudinal perspectives are brought in (Kappeler & van Schaik 2012).

Taxonomy and Biogeography

Baboons (Kingdon *et al.* 2013, Fleagle 2013) are large, predominantly terrestrial and quadrupedal Old World Monkeys with distinctive brow ridges and a distinctive "dog-like" snout, a feature to which the German vernacular "Hundsaffe" alludes to ("dog-monkey"). Baboons possess prominent ischial callosities – nerveless, hairless pads of skin that provide for sitting comfort. Baboons are highly sexually dimorphic, with males reaching twice the size of females and sporting large canines.

Baboons are distributed across sub-Saharan Africa, excluding the rainforests of West African and most parts of the central African rainforest. In addition, these monkeys also colonise parts of the Arabian Peninsula (Kingdon *et al.* 2013). There is no agreement on the taxonomical classification of the dozens of variant forms that have been described, not least because all appear to be interfertile. With respect to the hierarchical level of species or subspecies, the different taxa are sometimes assumed to constitute a single species (*Papio hamadryas*) (Groves 2001). Other authors, using more recent biogeographical and genetic data, distinguish six species, with more or less discrete biogeographical distribution (Zinner *et al.* 2011; see also Fleagle 2013,): Hamadryas or sacred baboon (*Papio hamadryas*), Guinea baboon (*Papio papio*), olive or anubis baboon (*Papio anubis*), chacma baboon (*Papio ursinus*), yellow baboon (*Papio cynocephalus*), kinda or Katanga baboon (*Papio [c.] kindae*).

Be it as it may, even the most elaborate species concepts will oversimplify a complex and dynamic evolutionary pattern (Jolly 1993). In any case, our study considers olive baboons (*Papio anubis*) as a separate species. The name refers either to the jackal-headed god Anubis of Egyptian mythology or to the olive or khaki-green coat colour, which characterises both sexes. Adult males have large manes, restricted to the foreparts and grading into shorter body hair, but not as sharply set off as in hamadryas or Guinea baboons. The face and skin around the callosities are dark grey to black. Nostrils project forward of the snout. One-fourth of the tail ascends before descending sharply as if broken.

Together with chacma and yellow baboons, olive baboons are characterised as "savannah baboons" (Jolly 1993) because the majority of populations are found in open habitats. Olive baboons populate the northern savannah belt, from Mali in the west to Eritrea and Ethiopia in the east, and southwards into Kenya and north-western Tanzania. They enter into true rain forest in the northern and eastern parts of the Congo basin, but not in West Africa. Hybridisation occurs with hamadryas at the Horn of Africa, and with yellow baboons in south-eastern Kenya and north-western Tanzania. The conservation status of olive baboons is "Least Concern".

Basic Baboon Socioecology

Generally classified as omnivores (for the following, see, e.g., Whiten *et al.* 1991, Hill & Dunbar 2002, Swedell & Leigh 2006, Ross *et al.* 2011), baboons do indeed feed on a wide range of plant foods (e.g., fruit, seeds, grass, roots). Given their relatively large body size, it is not surprising that baboons are able to tolerate a considerable degree of seasonality (van Schaik & Brockman 2005). Baboons can also range widely in response to changes in the environment (Alberts *et al.* 2005).

Nonetheless, while baboons are omnivorous feeders, this omnivory is combined with great selectivity (ibid.), with few items making up a high proportion of their diet. Fruit, whenever accessible, seems to be preferred to leaves, stems, or seeds, so that a high percentage of fruit in the diet appears typical (in particular also for olive baboons, Okecha & Newton-Fisher 2006). Baboons also prey on invertebrates (ants, termites, caterpillars), and, occasionally, lizards, fish and (mostly immature) antelopes, domestic goats and sheep, hares, birds and other types of monkey (Sommer *et al.* 2016).

Similar to their co-geners (except hamadryas and Guinea), olive baboons live in multi-male, multi-female troops averaging 15–150 individuals (for the following, see, e.g., Altmann & Alberts 2003, Swedell 2011, Alberts 2012). Troops are generally cohesive, but may break into smaller parties of variable composition during the day, a habitat that is increasingly viewed to represent a type of "fission-fusion" dynamics, analogous to the social organization of spider monkeys or chimpanzees. Females are philopatric, i.e. they remain in their natal troops, while males emigrate at sexual maturity. Both sexes tend to form a linear dominance hierarchy, with daughters often inheriting a dominance rank immediately below that of their mothers.

Activity Budgets and Ecological Constraints

The physiological causes and consequences of behaviour – e.g., energy requirements, life-sustaining metabolic processes, neuroendocrinological dynamics, intestinal turnover – are hard to measure under field conditions, although much progress has been made over the last couple of decades to obtain such information via faecal sampling (e.g., MacLarnon *et al.* 2015, for the Gashaka baboons). More straightforward are observational measurements of how behaviour is budgeted. Such records of activity patterns reflect physical and socioecological constraints and trade-offs between metabolic requirements and energy expenditure (Talebi & Lee 2010). For example, animals may reduce travel when energy is limited, or they may forage preferentially on high-quality foods.

Temperature and rainfall are two main components of habitat ecology. These affect the behaviour of animals not only directly, given the need of thermoregulation in response to varying degrees of heat and humidity (Hill 2006). The variables also affect animals indirectly, as they translate into variations in the abundance of food and availability of drinking water (Campos & Fedigan 2009).

Highly seasonal environments – like that of Gashaka Gumti National Park with periods of quite extreme heat, dryness and wetness (cf. *Ch. 03*) – are particularly challenging in this respect. Under these conditions, animals such as monkeys will be faced with trade-offs, e.g., whether to forage for the minimum amount of time necessary in each season to satisfy basic requirements, or whether to attempt to maximize the rate of nutrient acquisition, regardless of changes in food availability, while still aiming to minimise time and energy costs (Schoener 1971). Thus, habitat seasonality and particularly the spatial and seasonal changes in food availability is expected to highly influence the activity patterns and movements of the Gashaka baboons.

Models of habitat selection predict that, other things being equal, locales should be chosen that yield the highest average rate of energy intake (Stephens & Krebs 1986). However, while this may be applicable to rather mobile taxa such as birds or marine fish, monkeys do not have such choices, as they are attached to relatively fixed ranges that they cannot easily leave. Thus, prima facie, primate behaviour is constrained by the time available during waking hours and because certain activities cannot be executed simultaneously (Dunbar 1992). For example, time spent resting will go at the expense of foraging, travelling or socialising. These internal budgeting limitations will further be restricted by environmental conditions. Time spent feeding may be abridged with a higher percentage of fruit in the diet – given reduced need to process these relatively large and often clumped food stuffs (Hill & Dunbar 2002). Similarly, time spent travelling may increase with increasing group size, because individual food patches, other things being equal, will be more quickly depleted (van Schaik *et al.* 1983). Also, time spent resting in the shade is expected to increase when temperatures are higher (Hill 2006)

Travel Speed and Home Range Use

Related considerations apply to how much area animals need to "make a living", and how they move through the habitat they occupy (Johnson *et al.* 2015). An inverse relationship between habitat quality and home range size has been noted in a variety of reptiles, birds and mammals (Jones 1990), i.e. the better the habitat quality, the smaller the overall home range. Similarly, the temporal availability of food will impact on home range size (Dunbar 1988). Apart from just the extent of the area they traverse, animals, including primates, can be expected to adjust their ranging in relation to quality, distribution and availability of food.

As for the specific case of baboons, home ranges and group sizes are generally larger in open savannah habitats and tend to be smaller in more forested areas (Dunbar 1996). Such relations are brought about not just by patterns of food availability, but also because predation risk is more severe in open landscape. Larger groups offer more protection, through safety in numbers, as the individual chance of being killed is smaller (Hamilton 1971, Cowlishaw 1994), and through increased vigilance as the probability of detecting predators grows when group size increases (Pulliam 1973, Matsumoto-Oda *et al.* 2018). Moreover, access to shade and water will influence baboon home range size and moving pattern, given its importance in terms of thermoregulatory requirements – especially in the hot and dry environments typical of African savannahs (Barton *et al.* 1992).

Other things being equal, range size and ranging pattern should vary with group size (see above, van Schaik *et al.* 1983), given that competition for resources, whether they are water, food, safe spaces or resting spots, is higher in larger than smaller groups. Thus, intragroup competition is expected to lead to more extensive ranges and longer daily travel distances, given that the per capita reduction in resource density brought about by a greater head count necessitates increased efforts to ensure access for all group members (Barton *et al.* 1992; Chapman & Chapman 2000).

Crop-Raiding Versus Wild-Feeding: Costs and Benefits

Sustenance strategies will be greatly influenced by the spatial and temporal distribution as well as quality of food. "Stealing" from fields and gardens cultivated by humans is a foraging approach with very distinct costs and benefits (King & Lee 1987, Ross & Hill 2006, Ross *et al.* 2011). Thus, injury or even death might be inflicted by humans who defend their harvests – using prevention techniques such as shooting, poisoning and trapping. However, this risk, on average, is more than compensated by the fact that raiding is an extremely efficient foraging scheme (Warren *et al.* 2011). Crops are clumped both in time and space, which reduces search effort. Moreover, harvests such as maize, cassava or ground nuts need little processing time, as well as offering high concentrations of easily digestible carbohydrates, few digestion inhibitors, such as fibre, and fewer toxins (Strum 1994, Warren *et al*. 2011).

Cercopithecine monkeys in particular, such as macaques in Asia and baboons in Africa, are known to raid crops (see contributions in Paterson & Wallis 2005). Certain characteristics aid them to succeed in such ventures. They are generalist and opportunistic feeders, relatively terrestrial, large-bodied, and – not least – they possess cheek pouches, which allows to transport raided food to places of safety for further processing.

From this, we expect that the activity budget of crop-raiders should differ from their wild-feeding counterparts. Raiders are predicted to spend less time foraging and travelling, and hence have more time available to rest and socialise. On the other hand, crop raiding animals, similar to those provisioned by humans or those feeding on rubbish (Paterson & Wallis 2005), face increased competition and aggression because of the clumped nature of the food sources. Moreover, farmers perceive crop raiding animals as pests and chances are, that they will be killed (for examples of whole groups being wiped out, see Strum 1987, Sommer 1996, Paterson & Wallis 2005).

Study Aims

On the backdrop of hypotheses sketched out above, the present research will focus on the basic ecology of a crop-raiding troop of olive baboons in comparison with a wild-feeding troop living nearby. Emphasis will be on a comparison of activity budgets and home range use and its relation to habitat seasonality – with the ultimate aim to better understand the potential costs and benefits of engaging in occasional crop-raiding resp. living a life that depends entirely on natural resources.

MATERIAL AND METHODS

Study Troops

The main features of the two study troops are as follows (for reproductive behaviour and demographic development, see *Ch. 06*):

– *Crop-raiding troop (CR troop;* 10-20 animals). The home range near the village of Gashaka stretches along the wider banks of a major watercourse, the river Gamgam and consists of savannah-woodland, with patches of lowland forest and strips of gallery forest, plus agricultural fields. This group was previously referred to as "Gashaka troop" or "G [Gamgam] troop". CR's range is at an altitude of 320 m (Gashaka research station), with mean annual maximum temperature 33 °C and annual rainfall 1916 mm (cf. *Tab. 03.03*). The banks of river Gamgam have been largely cleared by small-scale farmers who grow crops such as maize, cassava, banana, mango, oil palm, yam, rice, sweet potatoes and groundnuts (Warren *et al.* 2011, Alberts 2012). The baboons raid harvests on 57 % of days when crops are growing in the fields, thus obtaining up to 50 % of their daily nutritional requirements (Warren 2003). Throughout their range, baboons are considered agricultural pests and crop damage can be substantial (Bennett & Ross 2011). Consequently, local farmers are known to have poisoned or shot study troop baboons. While crop-raiding constitutes a substantial proportion of CR troop's diet, we need to remember that the majority of food consumed by these baboons is still based on naturally occurring vegetation, supplemented by fractions of animal matter, mostly invertebrates (Sommer *et al.* 2016).

– *Wild-feeding troop (WF troop;* 25–37 animals). This group roams inside the national park in the Kwano study area. Previous publications referred to it as "K [Kwano] troop" or "NR [non-raiding] troop". WF's range is at an altitude of 583 m (Kwano field station), with mean annual maximum temperature 32 °C, and annual rainfall 2021 mm (cf. *Tab. 03.03*). WF's habitat – devoid of agricultural fields – consist to 68 % of forest and 22 % of woodland-savannah. The troop has little contact with humans, except when locals use an ancient footpath that transects their habitat. For diet, these baboons rely entirely on natural resources.

Data Collection

Data collection was coordinated by Caroline Ross, Roehampton University (director of baboon studies, *Gashaka Primate Project*). Results presented here were extracted from records for the 2004–2013 study periods, when both troops were regularly followed, often on a daily basis, by trained field assistants, students, senior researchers or volunteers.

The principal methodology entails focal-animal sampling. For this, adult females and some juveniles of both sexes served as focal animals, who were observed for 0.5–6 h per day (average 3 h). Every 15 min, the subsequent records were obtained as data points:

– basic activity of the focal ("states", i.e. travel, rest, forage; social interactions such as groom);

– identity of the focal animal's nearest neighbours, including their basic activity and distance (< 2, 2–5 m, > 5 m);

– scan data of the whole troop (habitat type, i.e. forest, savannah or grassland; number of animals visible to observer, surveying one's visual field from the far left to the far right; location as per GPS);

Ad-libitum records of specific, typically short, interactions ("events", as opposed to "states") were recorded at any time, i.e. not only during scans; these did not have to include the focal animal, but could involve any troop member; these interactions were categorised as unfriendly (aggression, displacement), friendly (grooming, embracing), sexual (presenting, mounting with or without thrusting), infant-centred (touching or handling infants).

The following analyses are restricted to

– the focal animal's general activity pattern (forage, rest, travel – "other" activities were omitted, as they occur relatively rarely; data for 2004–2011);

–distance travelled and home range use (GPS data for one full year, i.e. 11 months in 2012, supplemented by data for May 2013).

Data collection was more complete during some years and during the morning periods. Inconsistencies and gaps in the records result from idiosyncratic elements not atypical for long-term studies, such as staff absence, staff illness, adverse weather conditions, failure to find the study animals, as well as post-collection loss of records (some badly stored data sheets were eaten by rodents or drenched in bat urine…). Nevertheless, the data set used in this research is still quite large and should provide reliable analysis which can be compared to other long-term baboon field studies. Overall effort for the 2004–2012 study period is in the order of 3,000 h of observation.

General Activity Budgets

The annual and diurnal distribution of activity records are detailed in *Tab. 05.01*. Records for all years were lumped (see bottom lines of *Tab. 05.01*). In this way, a fair amount of records was available for all hours of the daytime and all months of the year, notwithstanding that certain hours and months were underrepresented during some periods. Data density for particular daytime hours ranged for WF troop from 118–3,108 scan points and for CR troop from 116–2,430 scan points. Data density for individual months fluctuated for WF troop from 538–1,946 records and that for CR troop from 624–1,976 records.

Care was taken to remove the bias of uneven diurnal and monthly distribution of observation records. Firstly, given the uneven distribution of sample points across daytime hours, the diurnal and annual records from absolute numbers were converted into *rates*. Secondly, when comparing entries for just foraging, resting and travel, these were considered to represent 100 %, and their respective proportion for each individual hour of the day during each individual month was calculated. To arrive at composite values for *diurnal* activity pattern, scores for a given daytime hour were then averaged across 12 individual months. Vice versa, to arrive at composite values for *monthly* activity pattern, scores for a given month were averaged across the 13 individual daytime hours.

Travel Distances and Home Range Utilization

During one full year (2012) GPS locations of focal individuals in both troops were logged on a handheld device (Garmin eTrex 10) every 15 minutes. The diurnal and annual distribution of GPS records is detailed in *Tab. 05.02*. From these, both travel distances and home range use were calculated via ArcView GIS version 3.2a with the Animal Movement Extension (Hooge & Eichenlaub 2000).

Distances were calculated by measuring the distance between two consecutive waypoints and converting them into rates per hour. Home ranges were estimated by applying the minimum convex polygon (MCP) method (cf. *Ch. 04* for details) to all waypoints logged for a specific period of time (e.g. dry season, wet season). A polygon enclosing 99% of the selected waypoints was used to account for outlier effect. Percentages of home range utilization were ascertained using a polygon enclosing 100% of the waypoints logged for each focal animal over the whole day.

Environmental Influences

The data for basic activities and home range use are related to environmental factors (see *Ch. 03*, for details on climate and plant phenology including measurements of abundance of tree and vine fruits). For this, monthly data on average temperature and rainfall were compiled for both the sites of Kwano (WF) and Gamgam (CR). Monthly records on fruit availability were only available for Kwano and used as a proxy for the Gamgam site. For the latter, qualitative records of the presence of certain crops – often raided by the baboons – were also available (*Fig. 05.02*).

Tab. 05.01. Annual and diurnal distribution of scan sampling data records for the two baboon study groups at Gashaka, 2004–2011(troop Kwano = wild-feeding; troop Gamgam = crop-raiding).6, 7…,17, 18 = daytime hours; Jan, Feb, …, Nov, Dec = months. Empty cells indicate that no records were taken (see text for further explanation)

(a) WILD-FEEDING

2004	6	7	8	9	10	11	12	13	14	15	16	17	18	Sum
Jan	23	32	32	36	36	35	33	33	13	13	16	20	5	327
Feb	7	12	12	12	11	16	15	16	9	3	4	4	1	122
Mar	16	20	21	21	25	31	29	27	21	16	21	24	5	277
Apr	37												4	41
May	63	56	52	42	16					8	34	50	11	332
Jun	73	58	60	55	28	16	5	11	15	16	43	44	2	426
Jul	48	50	60	37	20	15	8	14	15	17	41	38	5	368
Aug	38	38	40	40	26	13	12	24	24	24	29	22	2	332
Sep	67	68	65	65	41	29	19	28	29	29	53	62	12	567
Oct	58	61	60	60	34	21	10	15	16	19	41	44	10	449
Nov	65	69	64	52	29	12	7	8	8	7	21	41	10	393
Dec	54	66	66	56	31	21	17	15	14	9	34	35	4	422
Sum	549	530	532	476	297	209	155	191	164	161	337	384	71	4056

2005	6	7	8	9	10	11	12	13	14	15	16	17	18	Sum
Jan	6	33	43	38	15	8	4	3			9	21	5	185
Feb	24	57	60	62	37	21	8	6		5	22	43	11	356
Mar	27	47	45	43	17	8	8	6			15	29	8	253
Apr	22	37	43	43	24	17	9	6	8	9	23	24	9	274
May		7	25	38	34	36	10	7	13	12	13	8	3	206
Jun														0
Jul														0
Aug														0
Sep		8	9	12	4	2			2	4	4	4	1	50
Oct		39	36	22	7					25	24	32		185
Nov	12	17	14	15	13	12	3							86
Dec	7	17	20	17	13	12	2							88
Sum	98	262	295	290	164	116	44	28	23	55	110	161	37	1683

2006	6	7	8	9	10	11	12	13	14	15	16	17	18	Sum
Jan	15	60	60	45	36	32	8		4	4	6	8	2	280
Feb	4	12	12	12	8	8	8	8	8	8	7	8	2	105
Mar	24	56	54	51	46	46	11							288
Apr	10	34	42	41	42	36	11							216
May	2	32	40	43	37	27	7							188
Jun	1	28	32	32	23	17	4							137
Jul	4	25	33	36	33	32	8							171
Aug	1	4	4	13	8	8	2							40
Sep	3	31	38	38	34	30	7							181
Oct		26	43	44	35	29	7							184
Nov	2	16	17	17	17	16	4							89
Dec	3	29	32	32	32	29	14	15	14	12	16	12	1	241
Sum	69	353	407	404	351	310	91	23	26	24	29	28	5	2120

2007	6	7	8	9	10	11	12	13	14	15	16	17	18	Sum
Jan	11	59	67	68	70	56	11				3	5		350
Feb	5	53	51	51	54	50	26							290
Mar	14	62	57	63	63	59	33							351
Apr	32	68	65	66	66	50	23							370
May	24	61	67	68	64	52	31							367
Jun	4	35	40	40	28	16								163
Jul	6	59	60	56	31	6								218
Aug		13	24	18	11	5	1							72
Sep		37	48	43	16	2								146
Oct	2	37	47	39	18	1								144
Nov	6	36	40	39	27	10								158
Dec	11	26	31	28	25	7								128
Sum	115	546	597	579	473	314	125	0	0	0	3	5	0	2757

(b) CROP-RAIDING

2004	6	7	8	9	10	11	12	13	14	15	16	17	18	Sum
Jan	16	19	15	15	23	31	29	31	20	15	16	17	3	250
Feb	14	18	19	19	32	36	37	39	23	19	21	20	5	302
Mar	28	37	38	36	45	65	64	65	48	40	38	33	5	542
Apr														0
May	2	6	10	7	3						4	4	1	37
Jun	1	13	23	27	19	14	12	12	13	8	3	6	1	152
Jul	46	48	43	34	24	19	10	12	10	11	21	32	8	318
Aug	20	42	50	41	17	4	2	3	3	4	10	28	6	230
Sep	21	40	29	25	14	3		2	11	10	13	16	4	188
Oct	4	27	14	24	15	2			5	15	16	18	3	143
Nov	15	34	37	38	21	9	1	2	8	4	11	24	3	207
Dec	36	64	74	64	19	5	5	3	3	4	17	31	4	329
Sum	203	348	352	330	232	188	160	169	144	130	170	229	43	2698

2005	6	7	8	9	10	11	12	13	14	15	16	17	18	Sum
Jan	6	33	43	38	15	8	4	3			9	21	5	185
Feb	24	57	60	62	37	21	8	6		5	22	43	11	356
Mar	27	47	45	43	17	8	8	6			15	29	8	253
Apr	22	37	43	43	24	17	9	6	8	9	23	24	9	274
May		7	25	38	34	36	10	7	13	12	13	8	3	206
Jun														0
Jul														0
Aug														0
Sep		8	9	12	4	2			2	4	4	4	1	50
Oct														0
Nov	3	4	4	4	1							4		20
Dec	8	30	32	30	13	8	1							122
Sum	90	223	261	270	145	100	40	28	23	30	86	133	37	1466

2006	6	7	8	9	10	11	12	13	14	15	16	17	18	Sum
Jan	1	4	4	5	4	4	3	4	4	4	4		5	46
Feb	5	24	24	24	18	16	5	4	11	12	12	12	3	170
Mar														0
Apr														0
May														0
Jun														0
Jul														0
Aug														0
Sep														0
Oct														0
Nov	1	10	13	1	13	20	5							63
Dec	1	22	45	40	38	31	8	3	3	3	4	3	1	202
Sum	8	60	86	70	73	71	21	11	18	19	20	15	9	481

2007	6	7	8	9	10	11	12	13	14	15	16	17	18	Sum
Jan	3	37	44	54	41	32	13	3	3	4	3			237
Feb	1	25	35	37	41	41	11							191
Mar	9	56	73	75	71	67	19							370
Apr	1	28	42	47	41	39	12	6	7	12	10	9	1	255
May		5	36	46	58	64	34	29	21	16	8	4	1	322
Jun			8	30	42	38	9	8	6	5	5			151
Jul				11	19	21	15	9	11	11	11	7		115
Aug		6	7	11	14	10	3	9	11	12	10	8	1	102
Sep			13	26	32	23	5	11	16	15	5			146
Oct		2	10	21	28	26	7	10	10	9	4	4		131
Nov		5	23	28	35	26	14	12	15	17	21	12	3	211
Dec			5	8	6	9	3	2	7	9	6	10	3	68
Sum	14	164	296	394	428	396	145	99	107	110	83	54	9	2299

2008	6	7	8	9	10	11	12	13	14	15	16	17	18	Sum
Jan	1	47	53	53	56	58	32	3						303
Feb	0	55	66	71	67	64	54	12						389
Mar	14	60	62	59	61	49	19	1						325
Apr	32	72	68	67	66	61	28							394
May	16	33	34	41	32	36	24	2						218
Jun														0
Jul														0
Aug														0
Sep	11	35	42	30	11									129
Oct	5	26	28	19	6									84
Nov	3	20	22	15	4									64
Dec	3	25	28	18	3									77
Sum	85	373	403	373	306	268	157	18	0	0	0	0	0	1983

2008	6	7	8	9	10	11	12	13	14	15	16	17	18	Sum
Jan		8	18	4	12	15	9	7	14	13	12	12	5	129
Feb		6	22	35	26	19	4		6	9	10	10	6	153
Mar	5	41	62	58	43	30	6							245
Apr	22	59	53	40	39	26	16	4	4	1	3	1		268
May	2	13	15	20	8	15	13	3						89
Jun														0
Jul														0
Aug														0
Sep														0
Oct														0
Nov														0
Dec														0
Sum	29	127	170	157	128	105	48	14	24	23	25	23	11	884

2009	6	7	8	9	10	11	12	13	14	15	16	17	18	Sum
Jan	2	29	25	32	17	6	1							112
Feb	6	45	48	40	18	2								159
Mar	12	41	44	33	11									141
Apr	9	20	24	21	17	25	25	26	27	25	21	2		242
May	8	24	22	22	22	32	39	23	14	7	13	3		229
Jun	3	21	26	28	19	25	46	28	22	22	20	19	3	282
Jul		12	12	12	3									39
Aug		4	2		1	4	4	8	7	7				37
Sep														0
Oct														0
Nov														0
Dec														0
Sum	40	196	203	188	108	94	115	85	70	61	54	24	3	1241

2009	6	7	8	9	10	11	12	13	14	15	16	17	18	Sum
Jan		47	68	68	64	16								263
Feb		27	28	26	15	1								97
Mar	9	60	68	66	53	23	6							285
Apr	13	48	49	50	48	68	56	29	31	31	31	7		461
May	2	15	19	20	17	21	17	11	4	3	3			132
Jun	4	33	32	43	41	50	57	39	28	22	19	13	4	385
Jul	9	33	34	28	35	37	21	12	9	10	11	2		241
Aug		9	19	17	19	19	24	16	10	7	5	1		146
Sep		14	28	32	30	32	28	23	21	27	26	14		275
Oct		14	30	32	42	47	43	27	16	9	3			263
Nov		3	11	12	14	16	16	11	8	8	7	4		110
Dec		12	12	11	14	31	30	26	22	19	20	7		204
Sum	37	315	398	405	392	361	298	194	149	136	125	48	4	2862

2010	6	7	8	9	10	11	12	13	14	15	16	17	18	Sum
Jan	5	31	36	34	36	32	13	8	5	8	6			214
Feb	1	24	29	32	20	20	23	20	15	14	15	8	2	223
Mar	16	42	43	47	17	4	3							172
Apr	26	49	55	46	33	11	1							221
May	12	42	41	29	16	6								146
Jun	6	27	31	31	14	5								114
Jul	2	14	20	18	16	7								77
Aug	1	9	12	12	11	3								48
Sep														0
Oct	5	12	12	12	9	8	2							60
Nov	5	27	35	30	22	18	2							139
Dec	0	27	30	30	23	15	2							127
Sum	79	304	344	321	217	129	46	28	20	22	21	8	2	1541

2010	6	7	8	9	10	11	12	13	14	15	16	17	18	Sum
Jan		13	20	20	17	16	17	13	4	4	4	4	2	134
Feb	2	16	24	25	24	24	24	16	8	8	8	6	1	186
Mar	4	25	33	22	36	31	19							170
Apr	16	65	70	80	67	46	32	6						382
May	8	44	63	57	40	20	8	2						242
Jun	1	7	18	20	21	13	6	3						89
Jul		19	36	40	34	19	7	2						157
Aug		15	36	41	35	19								146
Sep														0
Oct		6	12	12	12	10	5	3						60
Nov	2	22	43	52	51	21								191
Dec	1	18	23	24	22	10								98
Sum	34	250	378	393	359	229	118	45	12	12	12	10	3	1855

2011	6	7	8	9	10	11	12	13	14	15	16	17	18	Sum
Jan		45	44	44	18	4	1							156
Feb		27	36	44	36	32	8							183
Mar	2	22	29	30	26	25	5							139
Apr	1	4	3	1	4	2								15
May			4	4	4	2	1							15
Jun														0
Jul														0
Aug			4	4	1									9
Sep	2	34	47	44	25	3								155
Oct	2	44	47	44	17	1								155
Nov	7	64	61	61	24	1								218
Dec	2	40	52	52	16	1								163
Sum	16	280	327	328	171	71	15	0	0	0	0	0	0	1208

2011	6	7	8	9	10	11	12	13	14	15	16	17	18	Sum
Jan														0
Feb	3	33	60	60	53	32	4	4						249
Mar	3	18	26	28	26	10								111
Apr	19	57	64	56	31	11	1	1						240
May	9	41	48	45	39	21	2	2						207
Jun														0
Jul														0
Aug														0
Sep	5	41	56	50	43	30	4	4						233
Oct	9	54	75	81	74	45	11	12						361
Nov	7	43	73	66	55	44	9	9						306
Dec	7	30	24	25	22	18	3	3						132
Sum	62	317	426	411	343	211	34	35	0	0	0	0	0	1839

Tab. 05.02. Diurnal and annual distribution of GPS sample points. (a) Wild-feeding troop Kwano (2012). (b) Crop-raiding troop Gamgam (2012; May data only are from 2013)

(a) WILD-FEEDING

Daytime	6	7	8	9	10	11	12	13	14	15	16	17	Sum
Jan	6	16	16	16	16	16	12	16	16	16	16	16	176
Feb	1	7	8	8	8	8	5	8	8	8	8	7	84
Mar	1	4	4	4	4	4	2	2	2	2	2	2	32
Apr	11	15	16	17	15	14	12	16	16	14	12	11	167
May	13	18	19	18	18	17	9	8	10	11	10	10	160
Jun	9	17	17	17	17	17	9	8	8	8	7	7	140
Jul	6	16	16	16	16	16	6	5	5	6	6	6	119
Aug	3	4	4	4	4	4	3	4	4	4	4	4	46
Sep	7	7	7	6	6	6	4	4	4	5	4	4	63
Oct	8	7	8	8	8	7	7	8	8	7	7	7	90
Nov	5	5	5	5	5	5	4	5	5	5	5	5	59
Dec	3	3	3	3	3	3	3	3	3	3	3	3	36
Sum	79	125	131	131	130	128	86	99	102	103	100	98	1172

(b) CROP-RAIDING

Daytime	6	7	8	9	10	11	12	13	14	15	16	17	Sum
Jan	2	6	6	6	6	6	5	5	5	5	5	5	62
Feb	3	8	9	9	9	9	5	9	9	8	7	7	91
Mar	1	5	5	5	5	5	3	5	5	5	5	4	52
Apr	8	10	10	10	10	10	7	6	6	6	6	6	95
May	8	9	9	9	9	9	8	9	9	9	8	8	103
Jun	4	5	5	5	5	5	5	5	5	5	5	5	59
Jul	8	8	8	8	8	8	9	9	9	8	7	7	96
Aug	5	5	5	5	5	5	4	4	4	4	3	3	52
Sep	7	7	7	7	7	7	7	7	7	6	6	6	80
Oct	7	7	7	7	7	7	4	4	4	4	3	3	62
Nov	8	8	8	8	8	7	7	8	8	8	8	8	94
Dec	5	5	5	5	5	5	5	5	5	5	5	5	59
Sum	63	82	84	84	84	83	68	76	75	72	68	67	904

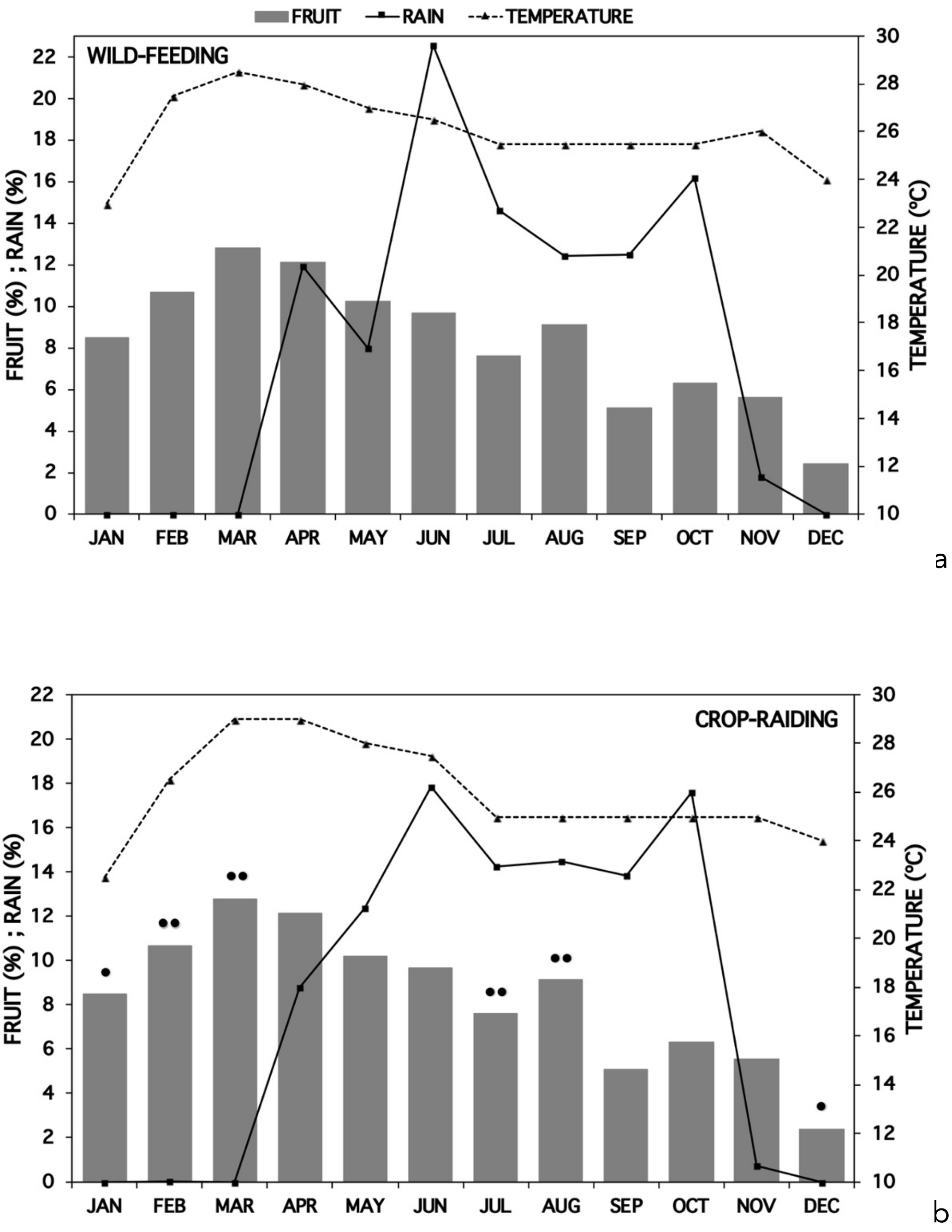


Fig. 05.02. Monthly temperature (average °C), monthly rainfall (% of annual total mm) and monthly fruit availability (% of annual total transect fruiting plants) in the Gashaka area during 2012 study year. (a) Wild-feeding troop Kwano. (b) Crop-raiding troop Gamgam (no specific data on fruit availability; months with considerable crop-raiding are indicated by black circles; one circle = moderate [stored maize, minor crops]; two circles = intense [fields with ripe maize stalks])

RESULTS

This section should be read against the general background that CR troop at times supplemented their diet with cultivated plants, while WF baboons only fed on naturally occurring plants (*Fig. 05.03*).

Fig. 05.03. Feeding behaviour of study troop baboons. (a) Member of crop-raiding troop Gamgam near village huts and fields. (b) Crop-raiding troop Gamgam scavenging from a maize store in a field. (c) Member of wild-feeding troop Kwano eating tree fruit. (d) Wild-feeding troop Kwano foraging in tree. (Photos: ©GPP, Adeelia Joffe [a], Ymke Warren [b], Adriana Lowe [c], Alejandra Pascual-Garrido [d]).

General Activity Budgets

Despite differing modes of sustenance, the figures for general activity budgets are very similar between the study troops and differ only by about a percentage point or so (*Tab. 05.03*). The combined average is foraging 44 %, resting 20 %, travel 19 % and other activities 7 %.

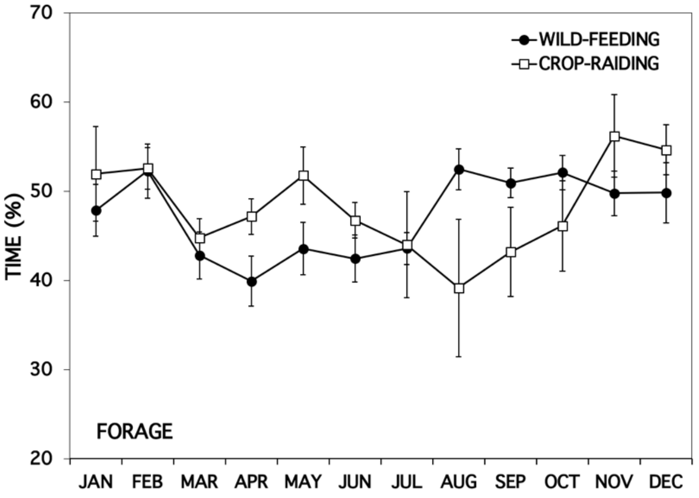
Tab. 05.03. Basic activity budgets for baboon study troops at Gashaka

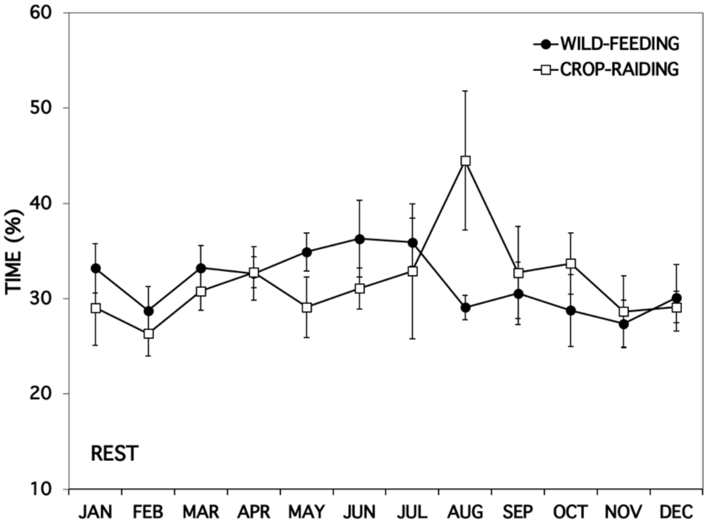
Activity (% scans)	WF	CR
Forage	43.1	44.4
Rest	30.2	28.9
Travel	20.2	18.8
Other (mostly groom)	6.5	7.9

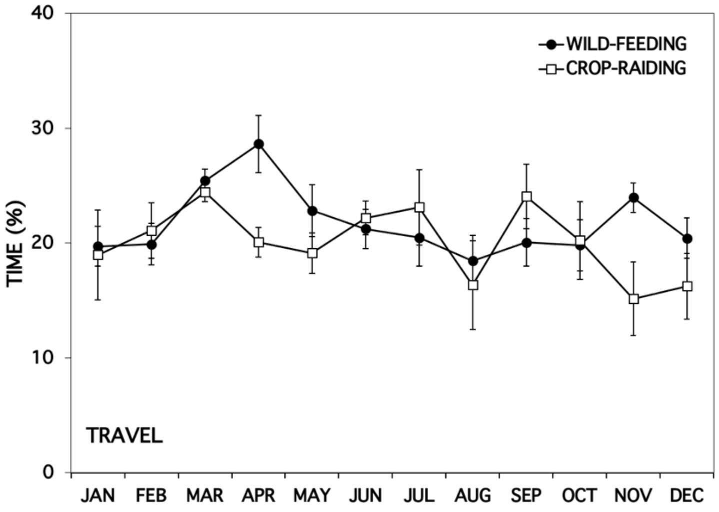
The following provides analyses of the diurnal and annual fluctuations of scores for the three main activities and compares them between troops. The diurnal patterns show very little difference (*Fig. 05.04a*). Daily activity patterns are similar between the two study troops and time spent foraging increases in both soon after sunrise. Between 07:00–16:00, foraging then always constitutes about 50 % of the daylight activity. It reduces again when the monkeys are about to settle for the night. An inverse pattern is observed for resting, which peaks during dusk and dawn, while taking up 30 % during the rest of the day. As for travel, minima are observed just after sunrise and around sunset, while travel takes up 20 % throughout the day (*Fig. 05.04b*).

In general, values for both troops are similar across the board for monthly scores, with only a few notable deviations (*Fig. 05.04a*); the annual distribution will be evaluated below in relation to environmental variables.

As a result, proportions of lumped data are likewise quite similar between the two troops, albeit CR troop travels significantly less than WF (p = 0.011; *Fig. 05.05*).


70
60
50
40
30
20
TIME (%)
WILD-FEEDING
CROP-RAIDING
FORAGE
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC


60
50
40
30
20
10
TIME (%)
WILD-FEEDING
CROP-RAIDING
REST
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC


40
30
20
10
0
TIME (%)
WILD-FEEDING
CROP-RAIDING
TRAVEL
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC

a

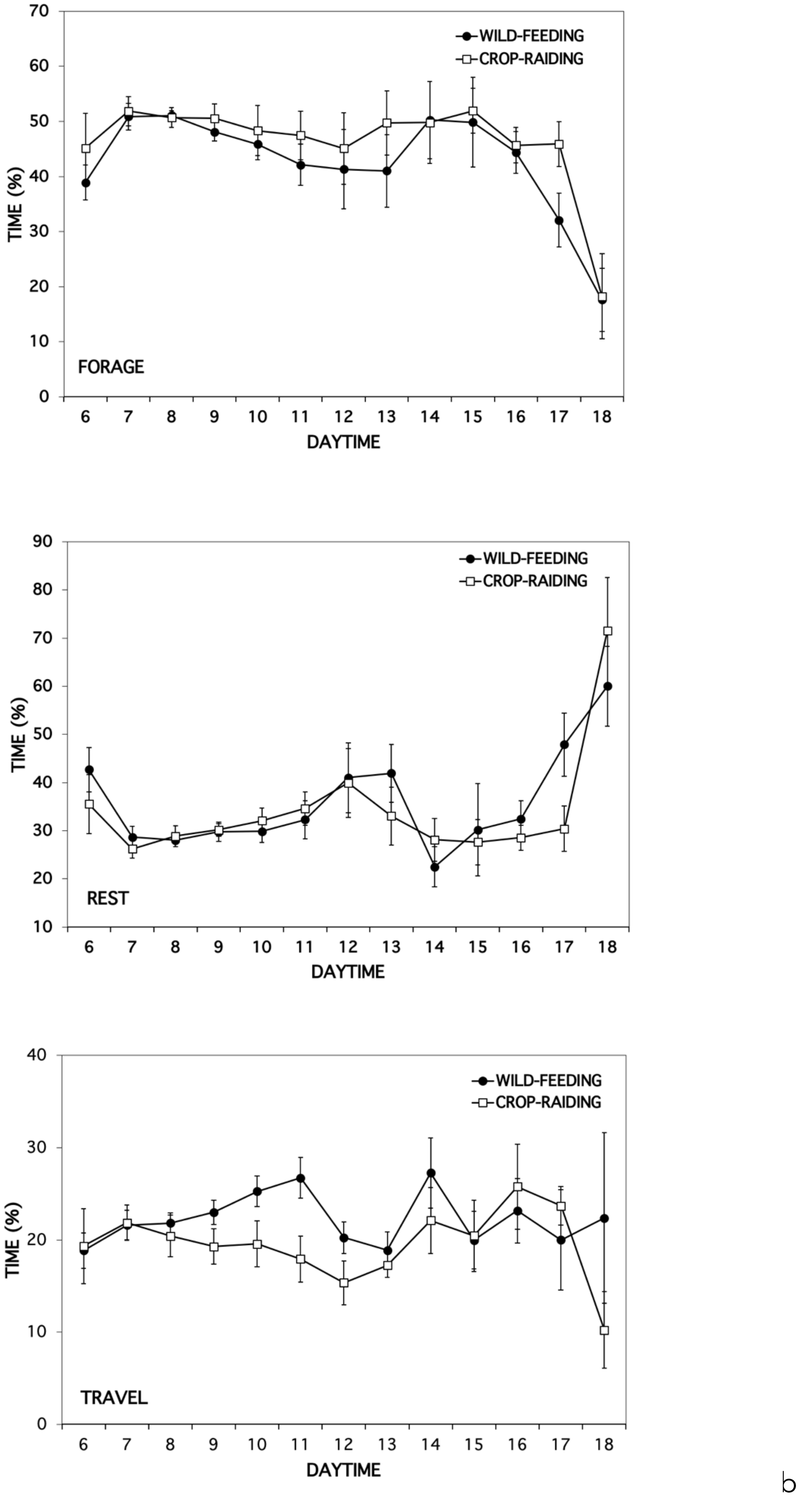


Fig. 05.04. Distribution of major baboon activities (forage, rest, travel) compared between wild-feeding troop Kwano and crop-raiding troop Gamgam (2004–2011). (a) Monthly. (b) Daily

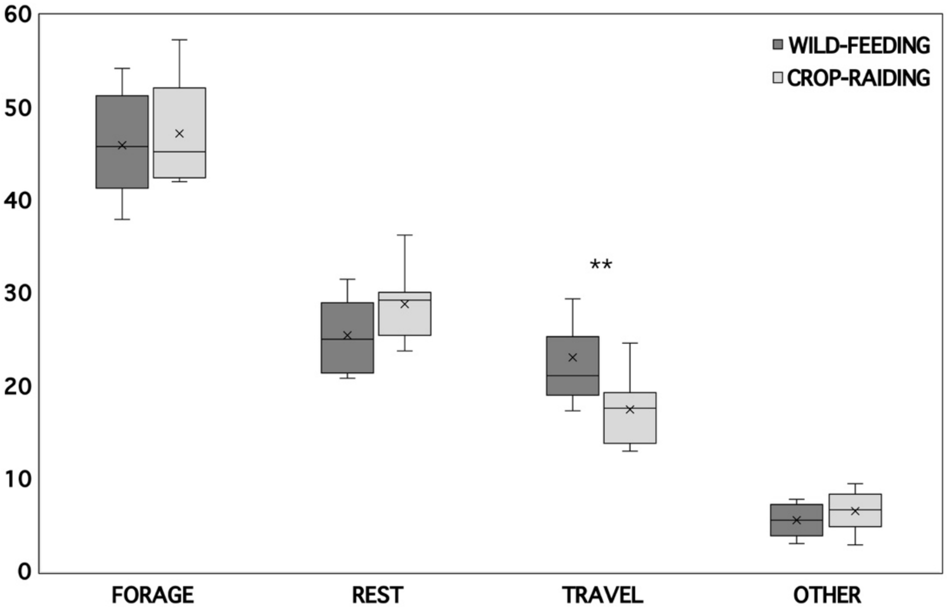


Fig. 05.05. Annual distribution of major activities (forage, rest, travel) compared between wild-feeding troop Kwano and crop-raiding troop Gamgam (2004–2011). Two Sample t-test: Forage t(11) = 0.789; p = 0.447 ns; Rest t(11) = 2.101, p = 0.059 ns; Travel t(11) = -3.076, p = 0.011 **; Other t(11) = 1.383; p = 0.194 ns)

Environmental Influence on Time Budget

In order to understand whether the environment in both troops differed, A MANOVA was performed comparing the two baboon study sites for environmental factors (rainfall, minimum temperature, maximum temperature). This revealed no significant differences (Pillai's Trace = 0.016, F(1,125) = 0.672, p = 0.571).

As there seemed to be no difference between sites in environmental elements, seasonal differences in activity budgets were also tested using the data for both troops combined. A MANOVA was performed comparing the overall activity between the dry and the rainy season (for definition, see *Ch. 03*). The test likewise returned no significant difference (Pillai's Trace = 0.008, F(1,119) = 0.314, p = 0.815).

Further tests were conducted to ascertain if activity patterns are influenced by external conditions. For this, major activity budgets (forage, rest, travel) were analyzed as a function of four major environmental factors (rainfall, minimum temperature, maximum temperature, fruit availability). Results are presented in *Tab. 05.04*. In summary, no overall pattern emerged, as of 24 tested effects, only 3 were significant. Thus, travelling time in WF troop went up when more fruit was available (p = 0.031), while in CR troop, travelling time went up when mean maximum temperatures were higher (p = 0.008). CR troop also spent significantly less time foraging when there was more rain (p = 0.040). There was also a trend indicating an increase in foraging time when more fruit was available.

Tab. 05.04. Single linear regression analysis of monthly values for each major activity (forage, rest, travel) as a function of the monthly values of four major environmental factors (rainfall, minimum temperature, maximum temperature, fruit availability). The respective linear regression models are conducted separately for WF and CR troops. Significant p values are emphasised in bold.

		Wild-feeding			Crop-raiding		
Variable (monthly averages)		Forage	Rest	Travel	Forage	Rest	Travel
Rain (mm)							
	F(df)	0.781 (1,73)	1.804 (1,73)	0.272 (1,73)	4.453 (1,51)	3.672 (1,51)	0.003 (1,51)
	R^2	0.011	0.015	0.004	0.081	0.067	< 0.001
	p	0.224	0.301	0.604	**0.040***	0.061	0.958
Minimum temperature (°C)							
	F(df)	1.683 (1,76)	0.007 (1,76)	3.799 (1,76)	3.066 (1,56)	3.151 (1,56)	0.274 (1,56)
	R^2	0.022	< 0.001	0.048	0.052	0.053	0.005
	p	0.199	0.932	0.199	0.085	0.081	0.603
Maximum temperature (°C)							
	F(df)	0.005 (1,76)	0.831	2.656 (1,76)	2.966 (1,56)	0.133 (1,56)	7.536 (1,56)
	R^2	< 0.001	0.011	0.034	0.050	0.002	0.119
	p	0.943	0.365	0.107	0.091	0.717	**0.008****
Fruit (%)							
	F(df)	1.649 (1,64)	0.180 (1,64)	4.898 (1,64)	3.950 (1,54)	1.051 (1,54)	2.243 (1,54)
	R^2	0.025	0.003	0.071	0.068	0.019	0.040
	p	0.204	0.673	**0.031***	0.052	0.310	0.140

Travel Distances

Environmental conditions also likely influence travel distances. This potential connectedness was already indirectly measured via time spent travelling. However, theoretically, animals may move very slowly, and thus technically spend a lot of time in locomotion, but would, in effect, only cover a small distance. Vice versa, they could move at higher speed, and cover a greater distance in a relatively short time. GPS data, on which the subsequent analyses are based, remove this bias, as they provide absolute measurements for distances crossed during a certain segment of time.

In the following, travel distances are compared with major environmental factors (rainfall, average temperature, fruit availability). Respective correlations are calculated separately for WF and CR troops.

It can be expected that measurements of travel distance per hour will be very similar, whether calculated across the individual 12 month of the year or across the 13 daytime hours (*Tab.*

05.05). As predicted, these values correspond very closely in both troops (WF, 215–238 m; CF, 147–154 m).

However, there are clear differences in travelling distances between the two troops (Two Sample t-test: t(22) = -2.496, p = 0.025). Thus, a monthly average of 215 m / h in WF troop compares to only 147 m / h in CR troop. Likewise, an average of 238 m / per daytime hour compares to only 154 m for WF troop.

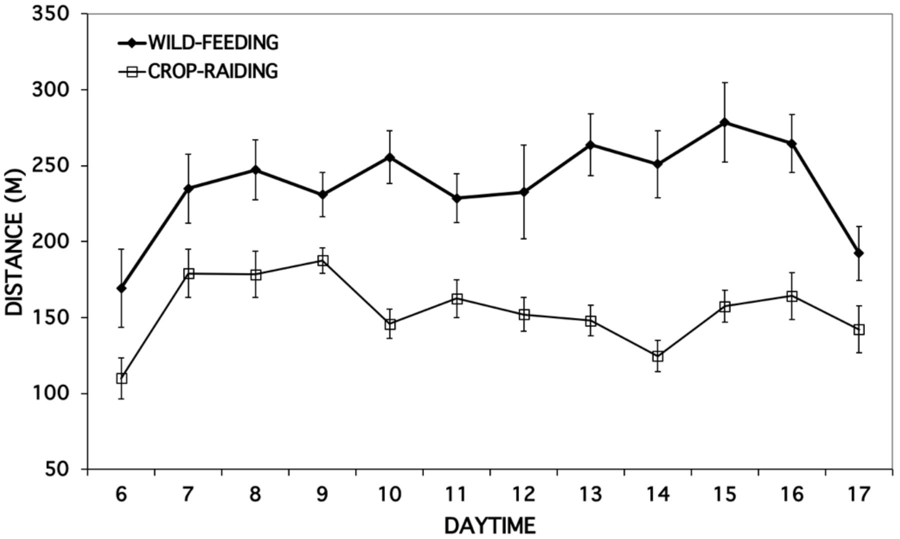
The diurnal pattern of travel speed (*Fig. 05.06a*) is similar for both troops. Hence, irrespective of markedly different baseline levels, monkeys of both troops begin and end their days moving slowly, while maintaining a more or less even pace throughout the day (07:00–16:00; cf. *Fig. 05.04b*).

Annual travel speed, i.e. distances covered throughout the year, is also similar for both troops (*Fig. 05.06b*). Thus, monkeys travel with greater speed when fruit is more abundant. A different measure might be expected to mirror this result, i.e. percent travel time per month (cf. *Fig. 05.04a*). Indeed, it does from WF troop, but CR troop is found to not increase travel time when there is more fruit available. Nevertheless, one needs to remember that time spent travelling is different from travel speed.

Tab. 05.05. Diurnal and annual breakdown of baboon travel distances (m / h) compared between wild-feeding troop Kwano and crop-raiding troop Gamgam (2012)

	Wild-feeding			Crop-raiding		
Month	Mean	Min	Max	Mean	Min	Max
Jan	260	5	903	115	18	483
Feb	223	6	623	173	2	726
Mar	231	2	677	164	25	1238
Apr	349	17	869	288	24	832
May	338	3	964	239	12	1279
Jun	159	4	668	131	13	504
Jul	158	6	544	153	24	793
Aug	220	5	917	127	22	665
Sep	175	16	584	100	14	646
Oct	173	37	569	114	15	559
Nov	167	10	765	84	0	304
Dec	129	3	219	78	15	336
Average	215			147		

Hour	Mean	Min	Max	Mean	Min	Max
6	169	3	764	110	2	569
7	235	6	820	179	28	726
8	247	11	964	178	13	707
9	231	23	545	188	18	1279
10	256	18	677	146	22	792
11	229	37	782	163	14	659
12	233	2	869	152	0	1238
13	264	12	811	148	16	645
14	251	22	903	125	16	443
15	279	47	917	157	15	587
16	265	28	796	164	17	562
17	192	12	614	142	15	793
Average	238			154		



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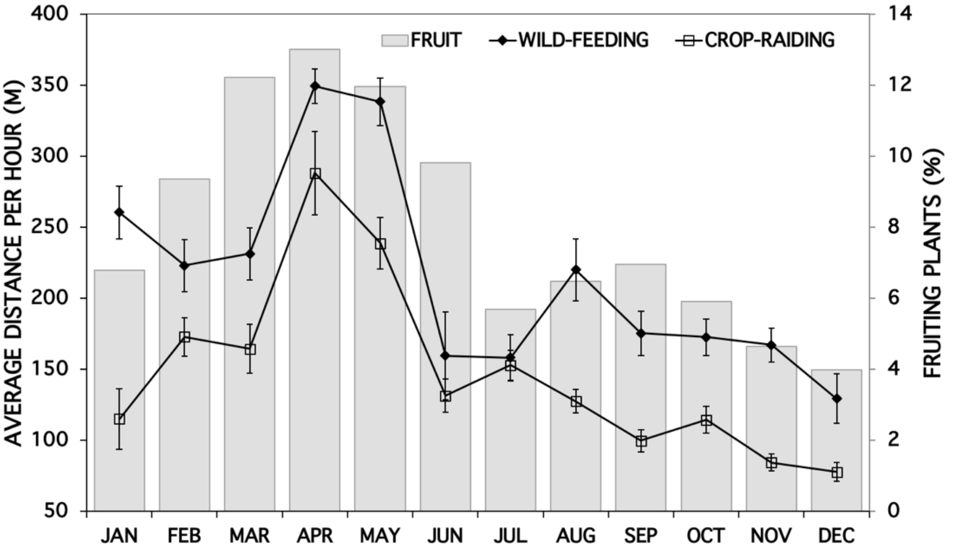

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Fig. 05.06. Travel distance (m / h) compared between wild-feeding troop Kwano and crop-raiding troop Gamgam (2012). (a) Daily. (b) Monthly

Next it was tested if basic environmental factors co-vary with travel speed. *Rainfall* showed no significant correlation (*Fig. 05.07*), while travel speed was positively correlated with average habitat temperature in the CR troop (p = 0.002; *Fig. 05.08*). Moreover, in both troops, fruit availability was positively correlated with travel speed (WF troop: p = 0.006, CR troop: p = 0.003), i.e. the monkeys moved faster when more fruit were available (*Fig. 05.09*).

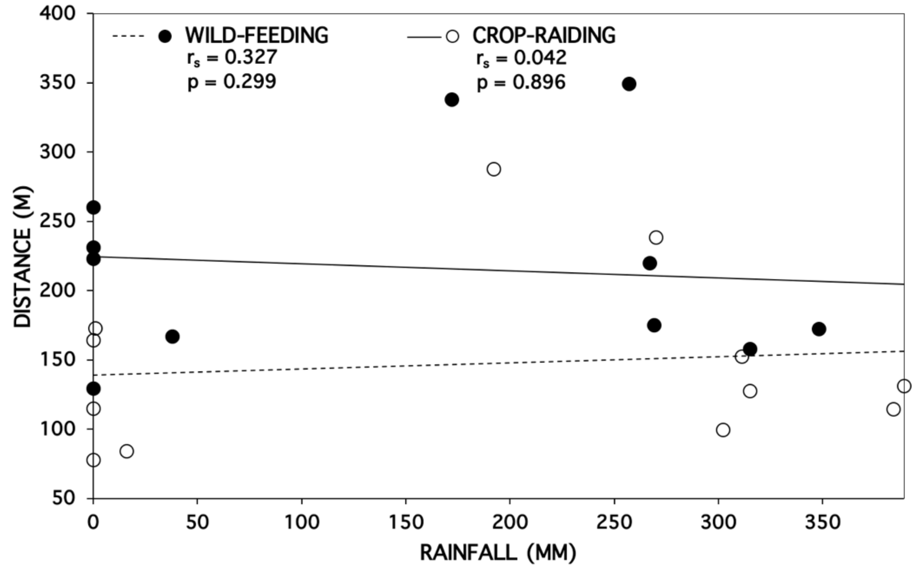


Fig. 05.07. Correlation between travel distance (m / h, monthly means 2012) and *rainfall*. Wild-feeding troop Kwano (Spearman's rank-order correlation: r_s = 0.327, p = 0.299 ns). (b) Crop-raiding troop Gamgam (Spearman's rank-order correlation: r_s = 0.042, p = 0.896 ns)

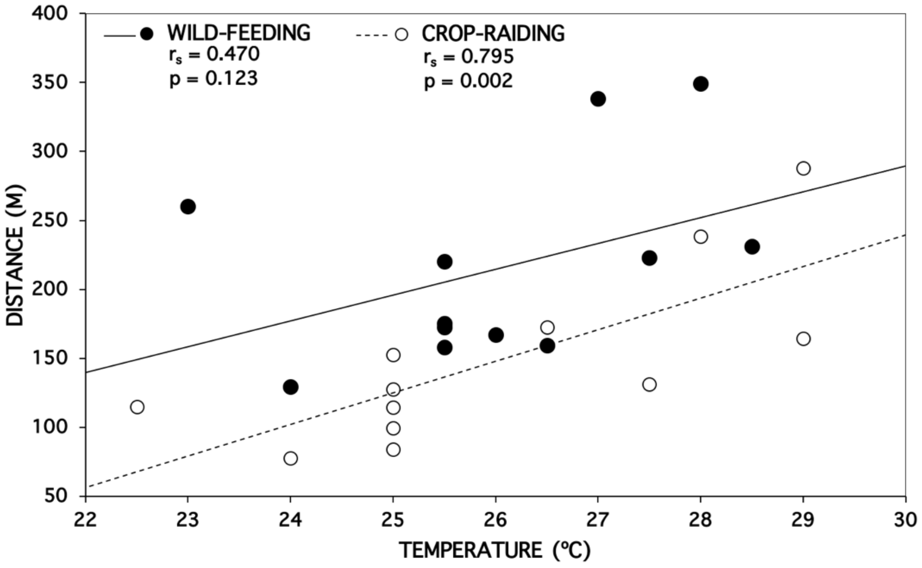


Fig. 05.08. Correlation between travel distance (m / h, monthly means 2012) and habitat average *temperature*. Wild-feeding troop Kwano (Spearman's rank-order correlation: r_s = 0.470, p = 0.123 ns). Crop-raiding troop Gamgam (Spearman's rank-order correlation: r_s = 0.795, p = 0.002**)

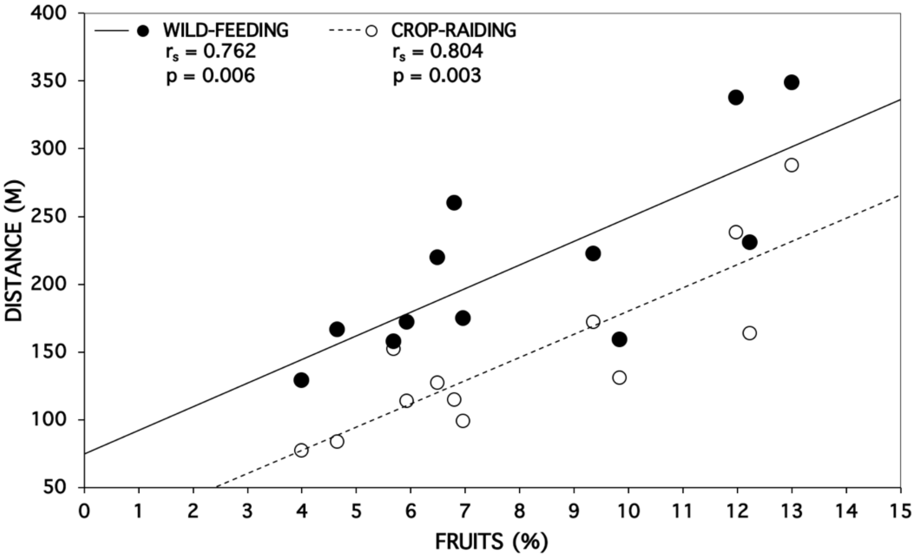


Fig. 05.09. Correlation between travel distance (m / h, monthly means 2012) and *fruit* availability. Wild-feeding troop Kwano (Spearman's rank-order correlation: $r_s = 0.762$, $p = 0.006$**). Crop-raiding troop Gamgam (Spearman's rank-order correlation: $r_s = 0.804$, $p = 0.003$**). Fruit availability measured via 8-km straight line transect at Kwano habitat, with no specific data for Gamgam

Home Range Utilization

The range utilization map generated from GPS waypoints for WF troop (*Fig. 05.10a*) shows an elliptic cloud of locations frequented by the baboons. Waypoints are quite evenly distributed throughout the forest-savannah mosaic, with no striking lacunae. The waypoints are, however, somewhat denser along the meandering banks of the perennially flowing small stream Mayo Dim (flowing from graph's upper right hand corner to its lower left hand corner).

The resulting map for CR troop (*Fig. 05.10b*) displays a discontinuous pattern. This is related to the large river Gamgam, which transects the troop's home range (flowing from the map's lower right hand corner to its upper left hand corner, with Gashaka village recognizable in the extreme upper left corner). GPS locations south of the river's extensive flood plains again form a continuous cloud. However, the northern boundary of the cloud displays a neat line of data points that look like a straight path. This accumulation of waypoints at the edge of the cultivation is caused by the fact that observers rarely followed the monkeys while these ventured into the fields in the flood plains. In this way, they avoided alerting the farmers, who will detect observers more easily than the crop-raiding baboons. (The ethics of such methodology might be questionable.) Instead, the observers overlooked the plains from vista points at the forest edge, thus avoiding that the monkeys were rapidly detected and chased away. A smaller cloud of GPS locations can be seen at the northern bank of the river, a forested area devoid of fields, where the baboons rest at times. Consequently, the GPS-based map for the CR troop range has few data points in the fields themselves. Nevertheless, waypoints engulf the cultivated areas, and therefore, calculations of the size of the CR home range are hardly affected.

In terms of size, the home range of WF troop (2.59 km^2) is somewhat larger than that of CR troop (1.86 km^2) (*Fig. 05.15*). The two troops differ in the extent of range use during different seasons. Accordingly, WF troop uses a smaller area during the wet season (1.51 km^2) compared to the dry months (2.05 km^2) (*Fig. 05.11a*). Conversely, CR troop criss-crosses a larger area during the wet season (1.43 km^2) compared to the dry months (1.11 km^2) (*Fig. 05.11b*).

While no in-depth analysis has been performed, it is intuitive that environmental influences will, on average, cause day journeys to be sometimes longer and sometimes shorter (for examples, see *Fig. 05.12*). The differential length of day journeys, across the year, will lead to smaller or larger areas covered by the baboons (*Fig. 05.13*). Nevertheless, a clear seasonal pattern cannot be discerned, meaning that area coverage is rather similar throughout the year. This is particularly true for CR troop, while values for WF troop fluctuate more, with a marked outlier in May.

The degree to which basic environmental factors affect home range use was also tested. In summary, no significant correlation was found between home range use and rainfall (*Fig. 05.14)* and fruit availability (*Fig. 05.16)*. A significant correlation was only detected for CR troop ($p = 0.032$), in that the daily area covered by the baboons increased with increasing temperature (*Fig. 05.15*).

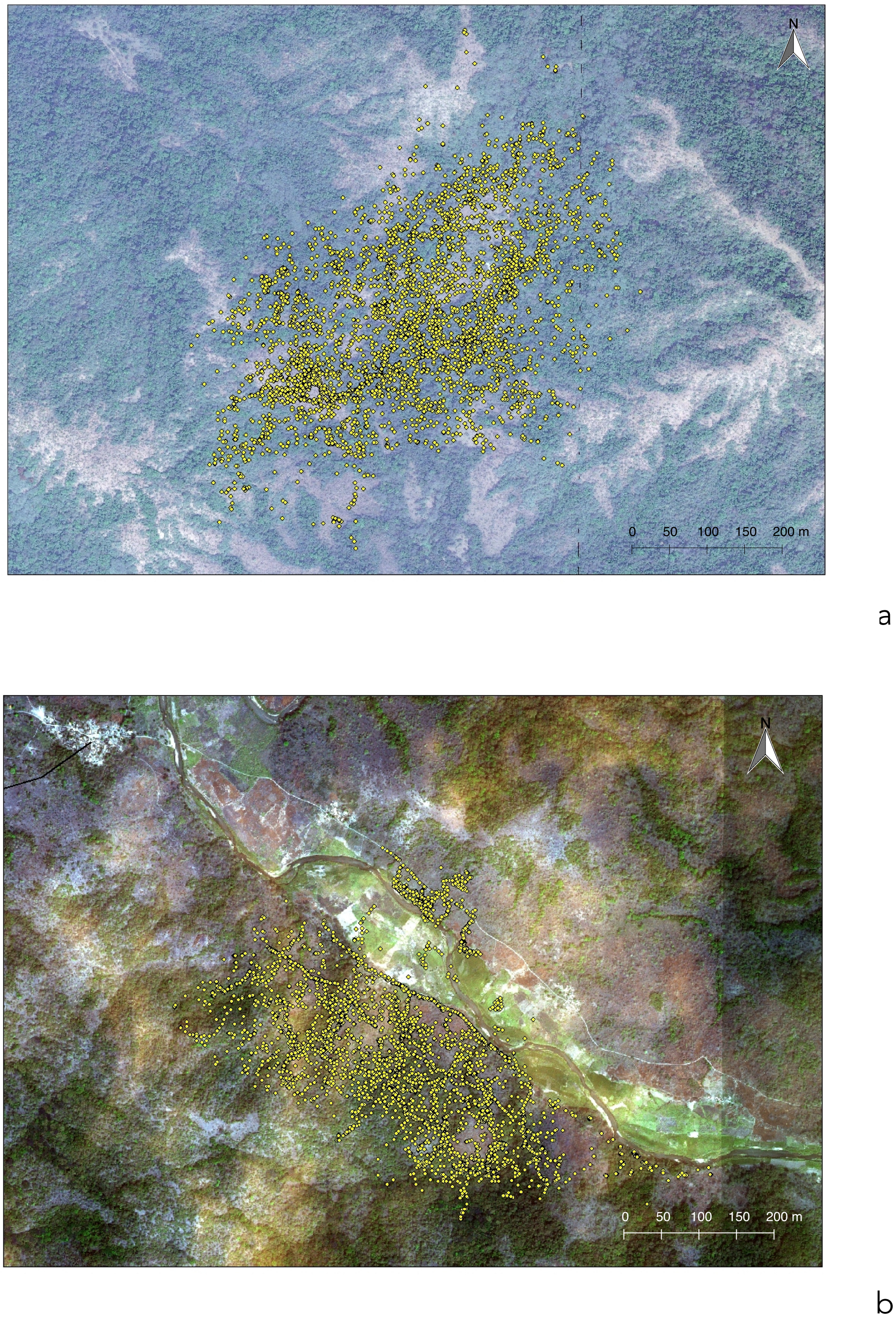
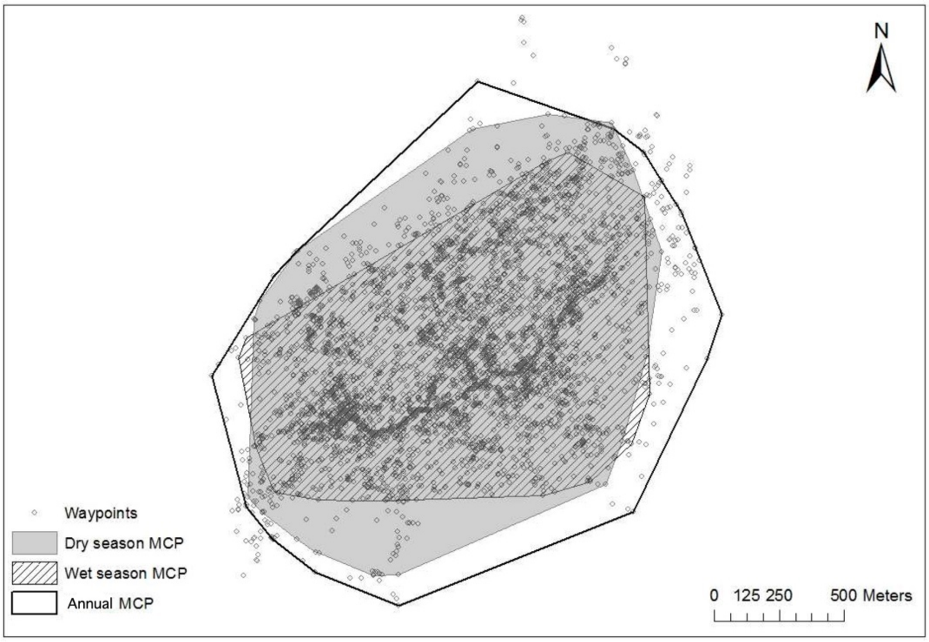


Fig. 05.10. Home range use of baboon study troops across one year (2012). (a) Wild-feeding troop Kwano. (b) Crop-raiding troop Gamgam (note: top left corner = Gashaka village; diagonal = River Gamgam, with fields along its banks). Satellite image of study sites overlaid with GPS points. (Design: GJ)



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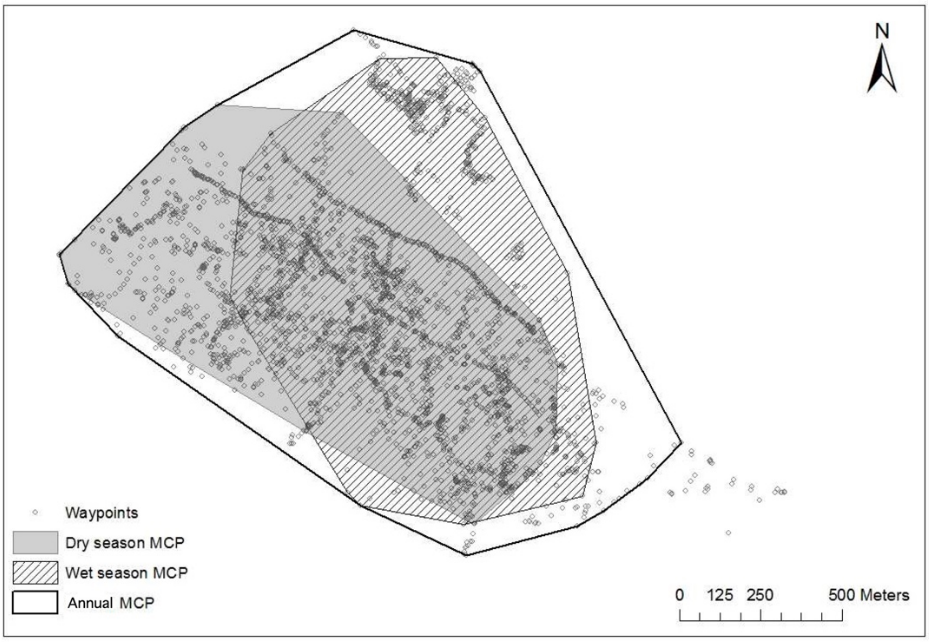


b

Fig. 05.11. Baboon home range use (2012), comparing 4 months of the dry season (Dec, Jan, Feb, Mar) with 4 months of wet season (Jun, Jul, Aug, Sep). (a) Wild-feeding troop Kwano (dry season area = 2.05 km^2, wet season area = 1.51 km^2, annual home range = 2.59 km^2). (b) Crop-raiding troop Gamgam (dry season are = 1.11 km^2, wet season area = 1.43 km^2, annual home range = 1.86 km^2). MCP = minimum convex polygon. (Design: GJ)

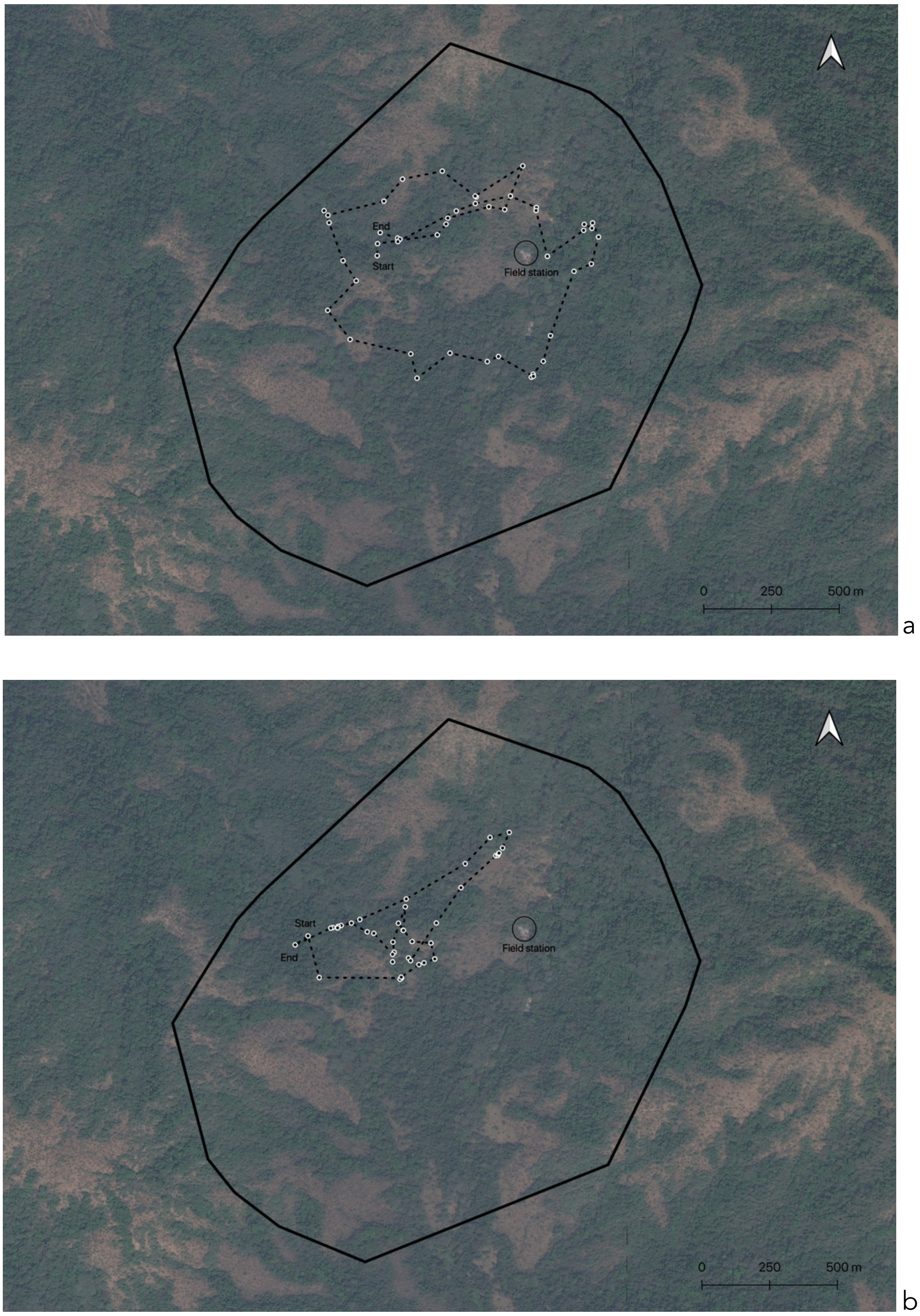


Fig. 05.12. Examples of long (a) and short (b) baboon day-journey of WF troop compared to 99 % minimum convex polygon of the annual home range calculation. (Design: GJ)

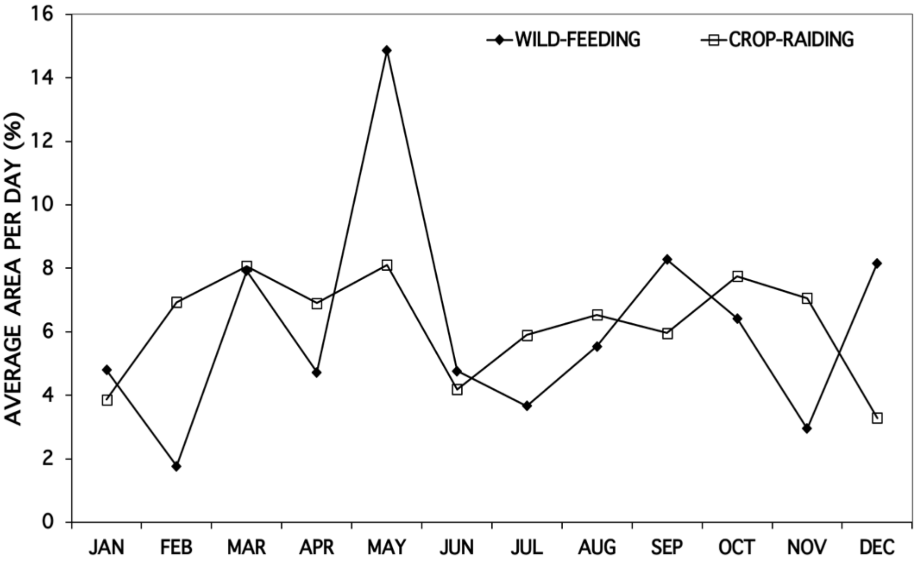


Fig. 05.13. Monthly area usage (% total home range area) compared between wild-feeding troop Kwano and crop-raiding troop Gamgam (2012)

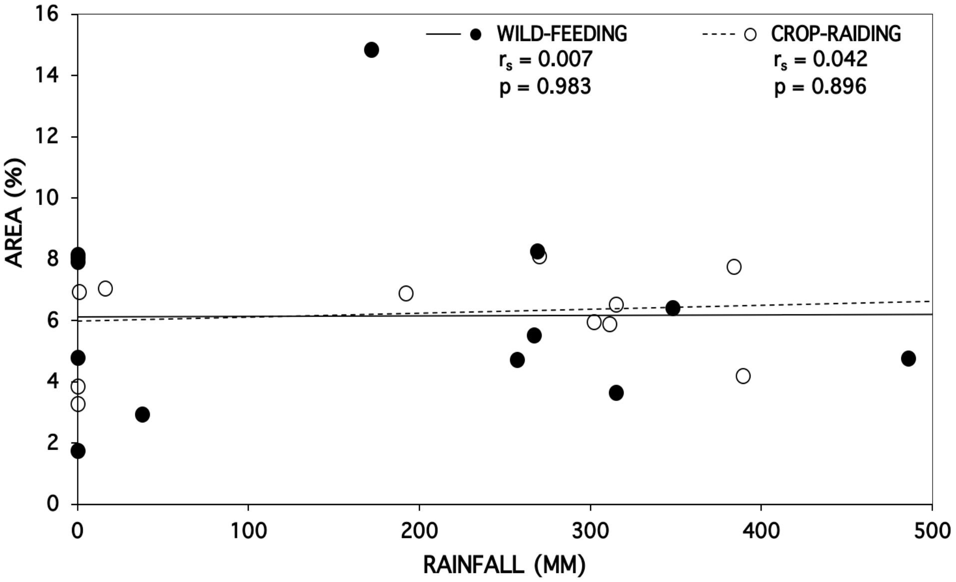


Fig. 05.14. Correlation between daily used home range area and *rainfall* (2012). Wild-feeding troop Kwano (Spearman's rank-order correlation: $r_s = 0.007$, $p = 0.983$ ns). Crop-raiding troop Gamgam (Spearman's rank-order correlation: $r_s = 0.042$, $p = 0.896$ ns)

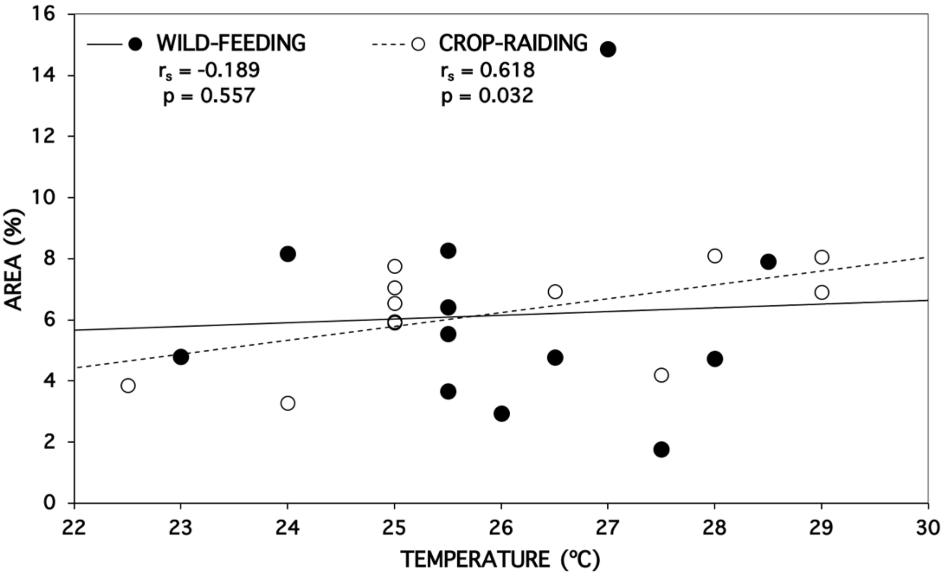


Fig. 05.15. Correlation between daily used home range area and *temperature* (2012). Wild-feeding troop Kwano (Spearman's rank-order correlation: r_s = -0.189, p = 0.557 ns). Crop-raiding troop Gamgam (Spearman's rank-order correlation: r_s = 0.618, p = 0.032*)

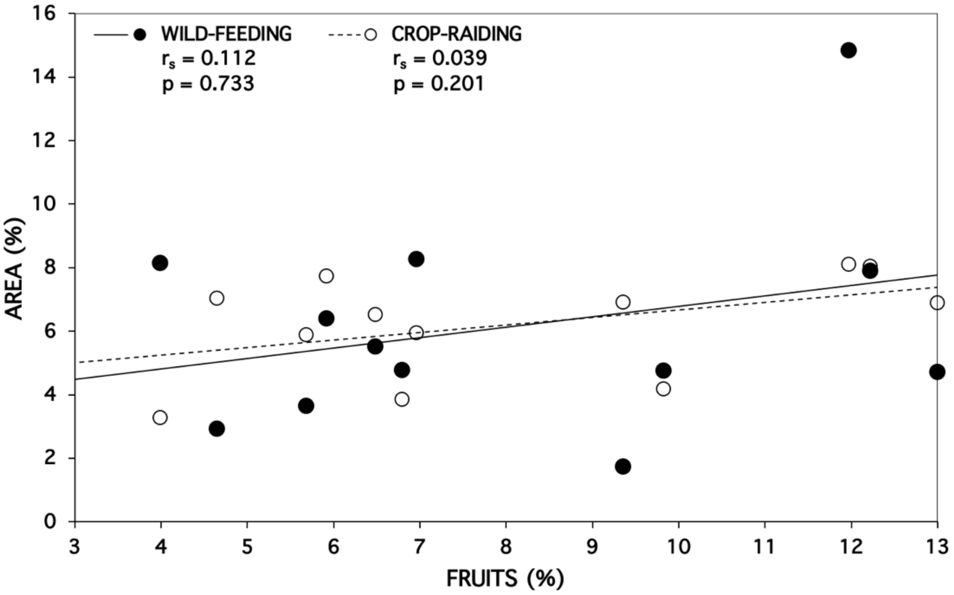


Fig. 05.16. Correlation between daily used home range area and *fruit availability* (as measured via 8-km straight line transect at Kwano habitat, with no specific data for Gamgam; 2012). Wild-feeding troop Kwano (Spearman's rank-order correlation: r_s = 0.112, p = 0.733 ns). Crop-raiding troop Gamgam (Spearman's rank-order correlation: r_s = 0.399, p = 0.201 ns)

DISCUSSION

Gashaka Gumti National Park is a geographical, climatic and habitat outlier within the distribution of olive baboons. Very high seasonal rainfall and home ranges that include large chunks of forest make this study site exceptional in comparison to most other research sites (Ross *et al.* 2011). Whether or not predation risk is lower within the Gashaka area than elsewhere is hard to judge – although leopards are certainly present till date (cf. *Tab. 02.04*), and baboons are also targeted by hunters.

We may therefore predict that the baboon behaviour reflects adaptation to such a "marginal" habitat. On the other hand, given the famed ecological plasticity of this monkey taxon, we should not expect a strict response – and even less so, if one compares a crop-raiding troop with a wild-feeding troop.

Overall Activity Budgets

The allocation of time to different behaviours by the two study troops can be expected to be influenced by the fact that CR baboons at times raid crops, whereas WF baboons only forage on natural foods (cf. *Fig. 05.03*). The inclusion of high quality foods from anthropogenic sources (such as farms) into diet should have a marked effect on activity budgets (van Doorn *et al.* 2010). Other things being equal, CR troop is therefore predicted to invest less time in foraging, given that crops represent clumped, high-quality food items, and to invest that time in resting. Travel time should likewise be shorter, and crop-raiders should also have comparatively higher rates of investment into social capital, such as engaging in grooming.

In fact, previous short-term research has largely found just that (*Tab. 05.06*). Three independent studies at Gashaka, none of them exceeding 1,000 hours of observation, found that foraging values for CR were 2–6 % lower than those for WF (27 vs. 31 %, 47 vs. 53 %, 43 vs. 45 %). The monkeys seem to reinvest the "saved" time to rest more, as values for CR were 1–7 % higher than those for WF (35 vs. 28 %, 20 vs. 17 %, 27 vs. 27 %). Two of the three studies also found, that CR monkeys spend less time travelling than WF (25 vs. 30 %, 21 vs. 20 %, 20 vs. 23 %), and two of the three studies also found higher "other" values (most of which consist of scores for allo-grooming) for CR (13 vs. 11 %, 11 vs. 11 %, 9 vs. 7 %).

Tab. 05.06. Basic activity budgets for baboon troops at Gashaka as measured during different studies: Generalized breakdown for wild-feeding troop Kwano and crop-raiding troop Gamgam. Values obtained by different studies are based on scan records; there is no overlap between those values and scan data used for the current study

Troop	Forage (%)	Rest (%)	Travel (%)	Other (mostly groom) (%)	Study years	Observation hours	Study period and references
Wild-feeding	31	28	30	11	2001–2002	454	Mar–Aug01, Nov01–Apr02 (Warren 2003, Higham 2006, Higham *et al.* 2009)
Crop-raiding	27	35	25	13		549	
Wild-feeding	53	17	20	11	2005–2007	455	Dec05, Feb–May06, Nov06–Apr07 (Ey & Fisher 2011)
Crop-raiding	47	20	21	11		370	
Wild-feeding	45	19	27	9	2009	536	Mar–Jun09, Aug–Dec09 (Lodge 2012)
Crop-raiding	37	28	28	8		473	
Wild-feeding	45	26	23	7	2009–2010	548	Mar–Jun09, Aug09–Mar10 (Alberts 2012)
Crop-raiding	43	27	20	9		375	
Wild-feeding	58	18	14	10	2012	216	Apr–Jun12 (Thompson 2012)
Crop-raiding						no data	
Wild-feeding	46	26	22	6	2004–2011	several	This study
Crop-raiding	47	28	18	7		1000s	

The current study, while results are generally similar in terms of the budget proportions of certain activities, did find far less pronounced differences between the troops. Thus, only the 4 % increase in travel time for WF represented a significant difference.

Methodological factors may have contributed to the less than perfect fit between short-term studies and the current long-term data, e.g., disparate definitions of age-classes as focal animals, a lack of certain months of data collection in the shorter studies, or different definitions as to what counts as "foraging". A more fine-tuned analysis reveals other potential reasons for the somewhat unexpected result. Thus, the short-term studies are heavily biased towards observations during the dry season months (76 %), whereas rainy season months are underrepresented (24 %). These biases were not always corrected by conversion into frequencies before arriving at figures for activity budgets. The current study is not subject to such distortions, as it is based on frequencies that cover each month of the year. Moreover, another explanation for the surprising disparity in the results might be that short-term data are likely to reveal differences, given that annual environmental variables tend to vary stochastically; e.g., a year may be particularly wet or particularly dry (*Ch. 03*). Such differences will, however, cancel each other out in a long-term data set which, in this way, will produce a more representative picture of a population (Kappeler *et al.* 2012).

Still, averaged across all observation periods and troops, most individual studies agree that foraging is the most prevalent activity (43.6 %, range 27–58 %), followed by resting (24.8 %, range 17–35 %), then travel (22.5 %, range 14–30 %) and other activities (9.2 %, range 7–13 %).

The diurnal distribution of major activities plateaus noticeable and with little variation between 07:00–16:00 (cf. *Fig. 05.04*). The hour just after sunrise (06:00-06:59) and lead-in period to the sunset (> 17:00) is associated with peaks in resting (as the animals are descending from sleeping trees resp. settle for the next night) and corresponding minima in travel and foraging. This finding is not in line with other studies who report, for other taxa, and early morning and late afternoon feeding peak, presumably related to prolonged overnight fasting (Talebi & Lee 2010). Still, measures of "feeding time" are very limited in their information content, given that animals may consume a high-quality food item within a very short time, while they need to process low-quality food over a longer period to obtain the same energy balance (*ibid.)*. Thus, to allow for a more meaningful comparison between different species and study sites, one would need samples other than crude "feeding-time" scores, i.e. information about actual energy intake.

A previous study at Gashaka (Lodge 2012, Lodge *et al*. 2013) attempted just that. The study collected data on 52 plant food items most commonly eaten by adult females of the two troops and assessed the amount of actual ingestion of particular foods, samples of which were analysed for nutritional content. As a result, it was found that the median energy intake rate of CR animals was 2011 kJ/h, almost twice that of WF animals with a median energy intake rate of 1041 kJ/h. These findings strongly suggest that crop-raiding has indeed nutritional benefits, with knock-on effects in terms of how raiders and non-raiders allocate time to basic activities.

The way primates move through their habitat is thought to be optimised so that they maximize energy gains (Chapman *et al*. 2012). Since energy intake is much lower for the WF troop, it was to be expected that the WF baboons adjusted their activity patterns, either by increasing foraging time and get more food or by increasing travelling time and search for foods with higher nutritional value (e.g. fruit), most likely at the expense of time spent resting or in social activities.

Whereas foraging rates are similar between the two troops, WF animals seem to spend less time resting and in social activities and spend significantly more time travelling (cf. *Fig. 05.05*), suggesting a preference for spread out foods with higher energetic value.

Seasonality of Activity Budgets

As both troops share very similar climatic conditions, the seasonal impact of general environmental factors should affect both troops in analogous ways. However, when testing both troops combined for differences in activity between dry vs wet season, there was no discernible difference. Climatic seasonality does not seem to influence the activity patterns of the Gashaka baboons in a pronounced way. Nonetheless, as mentioned before, one major difference between both troops is the proximity to human settlements and consequent access to crops of the CR troop.

Linear regression models – based on values for individual months of study, and conducted for both CR and WF troops separately – investigated the potential influence of rainfall temperature and fruit abundance on time budgets (cf. *Tab. 05.04*).

In general, there seems to be a trade-off in that the Gashaka baboons spend more time resting when feeding time decreases. The negative effect of rain on foraging time in the CR troop might be associated with the fact that several crops are planted when the rains start and that they continue to grow during the rainy season. Most crop-raiding takes place during the dry season when the plants are bigger and ripe (Dec–Mar, cf. *Fig. 05.02b*).

The increased time spent travelling when maximum temperatures are higher goes against an expected decrease in activity and respectively an increase in resting time as it was found in other baboon studies (yellow baboons: Stelzner 1988; chacma baboons: Hill 2006). However, the factors temperature and food abundance are at least partially confounded, because, at Gashaka, temperatures increase when the habitat produces more fruit and / or when fields yield crops (cf. *Fig. 05.02*). As a consequence, one can predict that time spent travelling will also increase in synchrony with increasing fruit availability and increasingly hot months (Johnson *et al*. 2015) – as the monkeys will move between rich, albeit spatially dispersed food patches.

Nonetheless, the increment in travelling time can also suggest a response to the more open habitat of the CR troop. This would mean that during the hotter periods, baboons would be moving more often between open and food rich areas (e.g. cultivated fields) and nearby forested areas which provide shade and are sought after during times of heat stress (Hill 2006).

Still, studies for other taxa have arrived at opposite results, e.g., that seasonally reduced fruit availability is connected with *more* travel, presumably to obtain alternative foods (Talebi & Lee 2010). Again, as mentioned above, one should remember that feeding time is a rather crude measure, because what matters for the animals is not so much the time needed to prepare and ingest food, but its quality in terms of macronutrients (e.g., Alberts *et al.* 2005; Lodge *et al.* 2013). In any case, detailed reconstructions of habitat architecture and associated travel constraints will be necessary to potentially disentangle such contradictions.

Baboons of other populations also invest less time in foraging during periods when they do not need to rely on harder-to-digest fallback food (Dunbar 1992, Alberts *et al.* 2005) or underground items like roots and tubers that require considerable processing time (Hill & Dunbar 2002). All these trends are in general accordance with foraging theory, according to which animals will spend longer periods at a feeding patch when the environment is relatively poor (Barton *et al.* 1992). Other constraints often found at baboon sites – such as problems with thermoregulation and access to water in a hot, dry, open environment – are mitigated at the Gashaka sites, because even during the 4–5 months with zero rainfall, water is always flowing in small streams and bigger rivers, while juicy wild fruit are abundant and fields yield crops (cf. *Fig. 05.02*).

Travel Speed

Averaged across the 4 values for daytime and months (cf. *Tab. 05.04*), the baboon troops covered, on average, 188.5 m per hour. There was, however, a marked difference, as CR's speed was slower (150.5 m) compared to WF's (226.5 m). This means that CR covered 76 m less per hour, i.e., CR's speed was only 66.5 % that of WF.

As a consequence, there is also a difference in home range size (cf. *Fig. 05.11*). Thus, WF's home range of 2.59 km^2 compares to CR's of 1.86 km^2 – meaning, CR's range is only 71.8 % of the size of WF's. The two values (66.5 % vs. 71.8 %) are rather close, and it seems reasonable to assume that CR indeed has to move less to cover the needs of nutrition and safety (sleeping sites). We can infer that CR's opportunity to supplement their diet with raided crops allowed them to cover less ground. This interpretation is supported by other studies who likewise found that baboons in human-modified habitats typically can access high quality and predictable food sources meaning within a smaller daily ranging distance (Johnson *et al.* 2015).

Moreover, CR troop is much smaller (10–20 members) compared to WF troop (25–37 members; cf. *Ch. 05*), and it is well established that smaller groups will cover smaller distances compared to larger ones (van Schaik *et al.* 1983; however, see Johnson *et al.* 2015).

Yet, an artefact of data collection may also have led to lower measurements of travel speed for CR. As explained in the results section, observers would at times not follow the baboons during their crop-raiding adventures, but – to avoid detection and thus reprisal from farmers – monitor troop movements from a "hide-out" at a nearby forest edge. This means, that GPS waypoints would also remain stationary during these periods.

Both troops cover less distance just after sunrise and before sunset (cf. *Fig. 05.06*). This coincides with the periods when the baboons are about to descend from their sleeping trees respectively settle for the next night.

As for travel speed during individual months, more distance was covered per hour when more fruit was available (cf. *Fig. 05.06b; Fig. 05.09*). It therefore seems that, during times of plenty, the animals use their mental map (Garber & Dolin 2014) to quickly move from one rich food patch to the next, discarding opportunities along the way to forage in less bountiful locations. Their overall movement will be faster, straighter, and more goal-directed (Johnson *et al.* 2015). This supports findings for other primate populations in that the proportion of fruit-based forage in the diet will lead to longer day ranges (ibid.), the rationale being that fruit tends to occur ephemerally in patches that are small, finite and distributed heterogeneously which renders them quickly exhaustible (ibid.). The energy spent travelling between fruit rich patches is likely compensated by the nutritional benefits of feeding on higher quality food (Hill & Dunbar 2002). During leaner times, the baboons proceed more slowly through the habitat. This may be, because they aim to conserve energy and / or rely more on fallback foods which require more search and processing time (e.g. underground roots, grasses), but are not as spaced out as fruit patches (ibid., Van Doorn *et al.* 2010).

These dynamics are true for both troops, despite the fact that CR troop can, to a degree, substitute wild fruit for raided crops.

The monkeys also tend to travel faster, if the ambient temperature is higher (cf. *Fig. 05.08*). This might be related to the need to move quickly across patches of open savannah and into the shade provided by large trees, so as to avoid long exposure to scorching sunlight. Such strategy might seem counterintuitive, as body heat increases during fast locomotion, and arboreal monkeys will indeed refrain from travelling when temperatures are high (Campos & Fedigan 2009). However, the baboon's terrestrial locomotion probably requires less energy than arboreal movements.

Home Range Use

The two study troops range about 11 km apart from each other, and their home ranges differ primarily because CR's encompasses agricultural fields (cf. *Fig. 05.10*).

Group size, diet and resource distribution are major factors determining baboon home range size (Dunbar 1996). As indicated above, WF troop always had more group members and relied entirely on more spatially dispersed food – and as a consequence, has a bigger home range (2.59 km^2) than CR troop (1.86 km^2).

However, the results are not in line with previous findings, which actually calculated a larger range for CR than WF (Warren 2003, Warren *et al.* 2011, Alberts 2012). Researchers related this, at least partly, to larger chunks of open savannah in CR's range. The discrepancy to this study findings might be due to the fact that CR's troop size declined markedly from 2012 (due to farmers increasingly killing the monkeys; *cf. Fig. 06.03*). Nevertheless, it is also possible that other studies used different methods in that they did not always cover a whole calendar year.

Differences between seasons within each troop's home range use were also noticeable (cf. *Fig. 05.11*). WF's range is 26.3 % smaller during the wet compared to the dry season (1.51 vs. 2.05 km^2), whereas CR's range is 28.8 % larger during the wet compared to the dry season (1.43 vs. 1.11 km^2). The smaller dry season range of CR troop might be related to the fact that more crops are available during that period (cf. *Fig. 05.02*). Thus, the baboons concentrate their foraging efforts on fields, and reduce travel in "natural" habitat. Notably, CR ventures only during the wet season into the forests at the northern bank of the river Gamgam; this means, that the monkeys cross the river when it carries most water. They achieve this by hopping onto large, tall rocks that still stick out from the stream.

Conversely, the larger WF range during the selected dry season months (Dec, Jan, Feb, Mar) coincides at least partly with increasing fruit availability. As indicated above, this may necessitate movements between rich, but spatially distant food patches. For future research, instead of using dry vs. wet months, it may be advisable to contrast months with the highest and lowest availability of fruit abundance – an analysis that may provide better insights into the influence of natural fruit abundance.

Overall, no straightforward correlation was found between monthly availability of wild fruit and home range use (cf. *Fig. 05.13*, *Fig. 05.26*), and also not for the variable rainfall (cf. *Fig. 05.14*). The variable temperature, as already indicated above, tends to positively correlate with home range use (cf. *Fig. 05.15*). This is perhaps driven by the necessity to avoid hot open spots of the savannah and move rather regularly into more forested, shady parts of the range – a need likely more pressing for CR troop (where we see a significant correlation) than WF troop.

Overall, the results add to the well-known fact that baboons are extremely adaptable monkeys that can cope with a range of environmental conditions, by adjusting their activity budgets and spatial strategies accordingly – similar to another type of versatile monkey, the Indian langur (*Semnopithecus entellus*, Little & Sommer 2002). In principle, the results obtained in this study support the idea that primates can buffer against temporarily adverse conditions by using one of two strategies (van Schaik & Brockman 2005), either (i) an *area switch* which means to trade increased travel distance and potentially greater risk against higher food abundance; or (ii) a *diet switch* by making do with food items that produce lower return rates, but require less travel time. However, despite a couple of decades of theorizing, primatologists still have a long way to go to produce the type of fine-grained data needed to answer these questions. In addition, the questions can be answered only through long-term data collected in comparable ways *and* applied to different populations (Kappeler et al. 2012).

Still, even the plasticity of the most ubiquitous monkey has limits – because Gashaka Gumti National Park constitutes the geographical edge of their distribution in West Africa. A short distance to the south, baboons are no longer found; instead, the rain forests of the Gulf of Guinea are inhabited by what seem analogous taxa in terms of size and lifestyle, primarily drills (*Mandrillus sp.*) and mangabeys (*Lophocebus sp.* and *Cercocebus sp.*; Oates *et al.* 2004).

CHAPTER 06

BABOON DEMOGRAPHY AND REPRODUCTION.

COMPARING WILD-FEEDING AND CROP-RAIDING TROOPS

Fig. 06.01. Anubis baboon study animals at Gashaka Gumti National Park. Depicted is adult female Sadiya (code F7, birth date unknown) with her fourth infant (code: M7.4), named Gonçalo (born 17Apr13). (03Mar14, photo: Amalia Pica)

INTRODUCTION

Baboons as Models for Human Evolution

Non-human primates have been extensively used as conceptual templates to reconstruct the evolution of human sociality (McGrew 2004, Cachel 2006). However, because many human traits are believed to have developed in open environments, our closest relatives, chimpanzees and bonobos, while allowing for a homologous perspective, are not necessarily the best models. Savannah-dwelling primates are thus seen as a better model, because these environments have less predictable climate between and even within seasons, and generally experience less rainfall (Alberts et al. 2005). In particular, distinct periodic changes in the obtainability of plant foods are viewed as major selective forces that shaped the lineages of early humans. It is for that reason that studies on savannah-living baboons have been employed as non-homologous models to explore the impact of ecological conditions on the evolution of human sociality (Strum 1987, Jolly 2001, Cheney & Seyfarth 2007). This comparison will often draw on the ability of humans to adapt to varied ecological conditions – a feature shared with baboons, given that no other non-human primate genus has such wide and diverse geographical range. The adaptability of the genus *Papio* is also reflected in another trait shared with the genus *Homo*: a basically non-seasonal pattern of reproduction (Alberts *et al*. 2005).

Within this framework, a multitude of investigations have explored the adaptive portfolio of baboons, compared populations and modelled ecological correlates of life-history behaviour, and demography (reviews in Alberts & Altmann 2006, Higham *et al*. 2009). However, detailed baboon studies are virtually restricted to populations of open grassland and savannah, mostly in East and South Africa. Few have looked at baboons in more closed, forested zones – given logistic difficulties of conducting such investigations as well as the fact that relatively few populations inhabit such habitats (see below).

The baboons of Gashaka Gumti National Park in Nigeria (*Fig. 06.01*) provide an opportunity to address this gap, given that this site is a geographical, habitat and climatic outlier (cf. *Ch. 05*). Studies of Gashaka baboons open up an interesting new perspective, because one wonders how the relatively forested habitat (*Ch. 03*) challenges the reproductive adaptability of baboons.

Baboon Reproduction

A brief introduction to baboon taxonomy, biogeography and socioecology was provided in the previous *Ch. 05* – while in the following, main features of reproductive biology will be reviewed as background for the current chapter.

Life-history traits of baboons have been described for various populations (e.g., Hill *et al.* 2000, Barrett *et al*. 2006, Higham *et al.* 2009, reviews in Sweddel & Leigh 2006).

Males undergo rapid growth in body mass with about 6 years, in their adult prime weighing almost twice as much as females. Males compete aggressively for rank and access to females. Although the mating system can be regarded as polygynandrous, there is reproductive skew, largely predicted by male dominance hierarchy. Decline in male dominance is accompanied by a decrease in testosterone and body-mass as well as mating opportunities (Altmann *et al.* 2010).

Females first give birth with about 5.5 years, after a gestation of 6 months. During their menstrual cycle, while approaching ovulation, female baboons develop a hormone-dependent ano-genital swelling, which can be so large as to increase female body weight by 14 % (Domb & Pagel 2001). Thus, swellings are energetically expensive (Anderson *et al.* 2006). The swelling expands to full turgescence (tumescence, inflation) during the follicular phase. Maximal swelling is then maintained, without much change, for several days. Increased progesterone production during the luteal phase initiates deturgescence (detumescence, deflation). Field workers have traditionally used the first day of detumescence to infer ovulation and day of conception when measuring gestation length (e.g., Altmann *et al.* 1977, Bentley-Condit & Smith 1997). However, endocrinological analyses based on faecal samples of Gashaka baboons established that detumescence can occur within a 5-day period after ovulation (Higham *et al.* 2008). Also, hormonal data of captive baboons established that ovulation usually occurred 2–3 days before deturgescence (Daspre *et al.* 2009). Females do not develop swellings during gestation or during the temporary sterility (lactational amenorrhea) associated with nursing babies.

The period of swelling (at times called "estrus" or "oestrus" – for a critique of the term, see Dixson 2013) coincides with certain female behaviours, from mood changes to aggression to affiliation (Ziomkiewicz *et al.* 2012). Often, females will form *consortships* with a particular adult male, who “herds” her away and mate-guards her against rivals. The pair thus spends much time in close proximity, including regular mating.

As for female mammals in general, sexual behaviour of female baboons can be conceptualized as comprising three dimensions (Beach 1976, see Dixson 2013, for review):

– *Attractivity* is embodied by the ano-genital swellings which triggers sexual interest in males.

– *Proceptivity* encompasses female behaviours aimed to entice males (presenting the hindquarters, lip-smacking, eyebrow-flashing, affiliative behaviours such as grooming).

– *Receptivity* includes the positioning of the body in response to male advances so that copulation and ejaculation can take place.

Already Charles Darwin linked the conspicuous signal to reproduction: “As these parts (…) become more brilliant during the season of love, I concluded that the colours had been gained as a sexual attraction” (Darwin 1876, p. 398). Nevertheless, while clearly related to sexual behaviour, the exact functions of ano-genital swellings are still a matter of debate (review in Zinner *et al.* 2004). Explanatory hypotheses tend to focus on female mating strategies with respect to (i) *reliable indicator* (females advertise fertility and quality via this costly signal), (ii) *many-males* (females maximise the number of mates to confuse paternity of offspring), (iii) *best-male* (females entice competition so as to recruit superior sires) or (iv) *single-male* (females elicit male investment via paternity certainty).

The explanations are not necessarily exclusive, because in many primate taxa, including baboons, females face the "female dilemma" (van Schaik *et al.* 2009). Hence, females are expected to strive to confuse paternity – thus pre-empting male-committed infanticide (review in Sommer *et al.* 2018) – while at the same time assuring paternity from a preferred male – so as to elicit male investment, also in the form of friendships (Smuts 1985). One strategy related to this would see females mate with several males whilst slightly swollen, whereas at maximum tumescence, consortships with individual and typically higher ranking males will occur more often (Higham *et al.* 2008).

Crop-Raiding Versus Wild-feeding: Costs and Benefits

Food-enhanced primates include populations provisioned by humans – because of tourism or religious reasons –, those that pilfer rubbish deposits, and those that raid crops from gardens and fields (Sommer & Mendoza 1994, Paterson & Wallis 2005, Ross *et al.* 2011). Obtaining clumped and energy-rich food in such efficient way has considerable implications for life-history variables, activity budgets, ranging and socialising.

Here, the focus is on a particular segment of food-enhancement, i.e. crop-raiding, by comparing a baboon troop that sets upon cultivated plants with a troop feeding exclusively on wild growing plants. Crop-raiding comes with distinct benefits and costs, as has been discussed in detail in preceding *Ch. 05* (for review, see Ross *et al.* 2011). Potential risks include injury (or even death) inflicted by humans who try to control crop-raiding monkeys through trapping, poisoning, as well as shooting. Temporary proximity of crop-raiders to humans and their livestock can also cause transmit diseases or ectoparasites (Nunn & Altizer 2006). Benefits include reduced time to search and process food, as well as nutritional benefits from ingesting easily digestible carbohydrates, less fibre and fewer toxins.

Potential consequences of crop-raiding resp. wild-feeding for activity budgets and home range use have likewise been explored in the preceding *Ch. 05*. Here, the focus is on life-history variables, i.e. the probabilities of survival and rates of reproduction at different stages of the life-span (Stearns 1992), as well as on the major variables that drive female reproduction (menstrual cyclicity, pregnancy, lactation. These analyses rest on the logic that (i) fitness components cannot all be optimized at the same time, (ii) an increase in one variable may lead to a decrease in another, so that (iii) organisms face decisions of how and when energy should be allocated. The outcome of these decisions are "trade-offs", such as those between growth versus reproduction, current versus future reproduction and current reproduction versus survival (Isler & van Schaik 2012). Some life history traits like gestation length are not very malleable, whereas a trait like the inter-birth interval can vary dramatically in response to environmental conditions.

As for the influence of crop-raiding (a factor related to improved allocation of energy; Lodge *et al.* 2013), one can expect accelerated deposition of subcutaneous fat, the fast-tracking of growth, with overall improvements of body condition and health, including higher parasite resistance. (However, as for the last point, there’s the need to consider that crop-raiders risk to catch anthropogenic parasites in the first place – leading to what might be a zero-sum game; Weyher *et al*. 2006). Ultimately, these benefits should translate into lower mortality of infants or adults.

Study Aims

Previous research looked at demographic and life-history traits of two baboon study troops (e.g., Warren 2003, Higham *et al*. 2009), by using data for a 7-year bracket (2000–2006) (Ross *et al*. 2011). While this is a considerable period, it is still a short-term period in relation to the reproductive period of a mammal that can live for decades. Using such relative restricted time-span may reveal associations between variables that are important for reproductive output, but it remains unclear if such relationships hold up over the long term (Chapman *et al*. 2017). Thus, the current study builds on previous findings, but utilises a much more comprehensive dataset by adding a decade of research. However, even a 16-year bracket (2000–2015) is not yet long enough to provide a complete picture, as it hardly equates to the typical life-span of baboons who have survived infancy. Still, the data do cover the entire lives of numerous individuals – and as such, their life histories lend themselves to provide relatively deep insights into evolutionary mechanisms (Clutton-Brock & Sheldon 2010, Kappeler *et al*. 2012).

Comparisons between the two study troops with very different foraging opportunities (wild-feeding versus crop-raiding) are expected to shed light on the influence of environmental constraints on intra-population reproductive pattern. In particular, this study aims to better understand if and how reproductive variables are influenced by seasonal rainfall and availability of fruit, as well as how life-history variables reflect trade-offs from crop-raiding versus wild-feeding foraging strategies. Hence, data presented here on the reproductive biology of the Gashaka baboons will be of considerable interest to understand the influence of the environment on the reproductive physiology and reproductive success of what has proven to be a highly adaptable taxon.

MATERIAL AND METHODS

For ease of reference, some essentials about the two study troops are repeated here – keeping in mind that home range use and activity budgets of Gashaka baboons have been analysed in *Ch. 05*.

– *Crop-raiding troop (CR troop)*. The first group lives near Gashaka village on the wider banks of the Gamgam river. In previous publications, this group is sometimes referred to as "Gashaka troop" or "G [Gamgam] troop". CR's range is at an altitude of 320 m, with mean annual maximum temperature 33 °C and annual rainfall 1916 mm (cf. *Tab. 03.03*).

– *Wild-feeding troop (WF troop)*. The second group roams inside the national park in the Kwano study area. In previous publications, it is sometimes referred to as "K [Kwano] troop" or "NR [non-raiding] troop". WF's range is at an altitude of 583 m, with mean annual maximum temperature 32 °C, and annual rainfall 2021 mm (cf. *Tab. 03.03*).

Observations of the troops (see *Ch. 05* for details) began in the year 2000. Since 2003, the troops were studied more intensively via data collection by trained local field assistants (FA), who may or may not have been accompanied by African and non-African students, researchers or volunteers. The baboons were typically followed for about 10–20 days per month, each observation period lasting about 6 h, from either 06:00–12:00 or 12:00–18:00. Data collection followed a sampling routine, resulting in a dense assortment of records. For example, between 2004–2011, data on WF troop amounted to 4,147 h and for CR troop to 3,596 h.

All adult troop members were known individually, as were many juveniles and infants, including most dates for birth, death, immigration and emigration (*Tab. 06.01*). Definitions of age–sex classes are described in *Tab. 06.02*. Moreover, for this study, females are categorised according to 6 reproductive states (*Tab. 06.03*). Fertilisation is assumed to have occurred 3 days before last day of the S3 period (D - 3) prior to pregnancy being noticed by researchers or birth. After one year of lactation, females were categorised as cycling, whether or not they had weaned their last offspring. Observed ano-genital swellings always took precedence over calculated states. For example, females who resumed swelling prior to the 1-year mark were marked as swelling and subsequently as cycling, rather than lactating. Common abbreviations used throughout the text are defined in *Tab. 06.04.*

The long-term observations produced increasingly detailed knowledge about troop compositions and matrilineal kin relations, for some individuals encompassing the entire lifespan from birth till death.

A noticeable lack of information concerns paternity. Faecal samples – which will allow to generate these data – have been collected for most individuals, however, they are not processed as yet. There are plans to work on this in collaboration with Leslie Knapp, previously at the University of Cambridge, now at The University of Utah.

Tab. 06.01. Members of baboon study troops (date of reference 10Mar15). Troop: WF = wild-feeding troop Kwano; CR = crop-raiding troop Gamgam. Name: Random name given by researchers; however, yearly cohorts of monkeys born since 2006 begin with the same letter, i.e. 2006 = A, 2007 = B, etc.; NN = not named. Short: Three-letter abbreviation of name. Sex: F = female, M = male, U = unknown. Code: Adult females and adult males are labelled by a number. Known offspring are denoted by their mother's number and a second number that represents their rank in the birth order since the study began in 2002. E.g., the second known offspring of female 2 is 2.2. If this is a female, her first offspring would be labelled 2.2.1. Birth: As known to the nearest day or range of days. Immigration: Nearest date to when new males are recognised as having joined the troop. Death: (+) = dead body found; all other dates refer to last sighting. Emigration: Refers to transfers of adult males from the Kwano troop, either primary (as Kwano was the natal troop), or secondary (if males were immigrants). Some of these males may have died and not emigrated.

Troop	Name	Short	Sex	Code	Birth	Immigration	Death	Emigration
WF	Bera	bra	f	1			2014	
WF		NN	m	1,1	3-Jun-02		08-Jan-03 (+)	
WF		NN	u	1,2	17-Mar-04		Apr-04 (+)	
WF	Jamilu	jmu	m	1,3	10-Jan-05			21-Feb-15
WF	Bary	bry	m	1,4	30-Jun-07		29-Sep-09	
WF	Fadi	fdi	f	2				
WF	Ann	ann	f	2,1	24-31 Oct-06			
WF	Helen	hln	f	2.1.1	6-Jan-14			
WF	Dandy	dnd	m	2,2	8-Feb-09			
WF	Elena	ele	f	2,3	Dec-11		4-Dec-12	
WF	NN			2,4	26-Sep-13	7-Oct-13		
WF	Harrison	hrs	m	2,5	30-May-14			
WF	Kaiye	kye	f	3			20-Dec-11	
WF	Faro	far	m	3,1	6-Jan-06			24-Nov-13
WF	Doris	drs	f	3,2	21-Aug-09		20-Dec-11	
WF	Ladi	ldi	f	4			3-Feb-15	
WF	Karima	krm	f	4,1	18-Aug-02		10-Sep-09	
WF	Baki	bak	m	4,2	2004			27-Nov-12
WF	Andy	ady	m	4,3	14–16-Dec-06		24-May-10	
WF	Debbie	deb	f	4,4	31-Aug-09			
WF	Fane	fan	f	4,5	2-Sep-12		19-May-13 (+)	
WF	Lami	lmi	f	5			Dec-12	
WF	Nawa	naw	m	5,1	2005			

(cont.)

(cont.)

Troop	Name	Short	Sex	Code	Birth	Immigration	Death	Emigration
WF	Beth	bth	f	5,2	14–21-Aug-07			
WF		NN	u	5,3	Oct-10		02-Nov-10 (+)	
WF	Momi	mom	f	6				
WF	Amy	amy	f	6,1	3-Sep-06			
WF		NN	u	6.1.1	5-Nov-13		11-Nov-13	
WF	Hery	hry	m	6.1.2	9-Sep-14			
WF	Bola	bla	f	6,2	3-Feb-08		1-Sep-08	
WF	Eric	erc	m	6,3	Oct-10			
WF	Happy	hpp	f	6,4	26-Jun-14			
WF	Sadiya	sdy	f	7			3-Feb-15	
WF	Tala	tal	f	7,1	20-Jan-06			
WF	Giulia	gla	f	7.1.1	24-Dec-13			
WF	Daji	dji	m	7,2	3-Aug-08			
WF	Eto'o	eto	m	7,3	1-Mar-11			
WF	Goncalo	gcl	m	7,4	17-Apr-13			
WF	Tojali	tjl	f	8			Dec-09	
WF	Rabi	rab	f	8,1	21-Dec-03		Apr–Sep-11	
WF	Eggi	egg	m	8.1.1	6-Mar-11		1-May-11	
WF	Comfort	cft	f	8,2	19-Apr-08		1-Sep-09	
WF	Ymke	ymk	f	9			21-Feb-15	
WF	Murna	mur	f	9,1	12-Jul-05			
WF	Ghana	ghn	m	9.1.1	24-Apr-13			
WF	Duna	dna	m	9,2	Aug-08		2-Nov-09	
WF	Emma	emm	m	9,3	Sep-10			
WF	Gaetane	gat	f	9,4	29-Nov-13			
WF	Dr. Kate	drk	f	10				
WF	Beni	bni	f	10,1	4-Jun-07			
WF	Dimi	dmi	m	10,2	10–14-Dec-09			
WF	Grace	grs	f	10,3	30-Sep-13			
WF	Dogo	dgo	m	1			24-Jun-09	
WF	Sanda	snd	m	2			20-Feb-12 (+)	
WF	Addo	add	m	3			Nov-05	
WF	Boka	bka	m	4			Apr-03	
WF	Sobo	sob	m	5			Dec-03	
WF	Doro	dro	m	6		Oct-05	08-Sep-09(+)	
WF	Kasa	ksa	m	7		Dec-06		
WF	Sama	sma	m	8		Dec-06	8-Dec-11	
WF	James	jms	m	9		Feb-07		27-Feb-08
WF	Bonny	bon	m	10		Feb-07		Sep–Oct-10
WF	Jolly	jol	m	11		Feb-07		Feb-09
WF	Boka	bok	m	12		2-Apr-07		
WF	Damina	dmn	m	13		2008		17-Jun-09
WF	Darin	drn	m	14		Jan-09		Apr–Sep-11
WF	Dali	dli	m	15		Jan-09		
WF	Erni	ern	m	16		Sep-10		
WF	Figo	fig	m	17		Jan-11		
WF	Garrido	gro	m	18		Nov-13		

(cont.)

(cont.)

Troop	Name	Short	Sex	Code	Birth	Immigration	Death	Emigration
CR	Budurwa	buw	F	1	aprox. 1997			
CR	Peter	pet	m	1,1	Nov-02			
CR	Fedi	fed	m	1,2	Mar-05		May-11	May-11
CR	Bill	bil	m	1,3	Nov-07		May-10	May-10
CR	Eto'o	eto	m	1,4	Mar-10			
CR	Mamakane	mmk	f	3	aprox. 1990		Dec-10	
CR	Kane	kan	f	3,1	Oct-00			
CR	Kofa	kof	m	3.1.1	Dec-05		Mar-11	
CR	Bintu	bin	m	3.1.2	May-07		May-09	
CR	Diana	dia	f	3.1.3	Aug-09			
CR	Emose	emo	m	3.1.4	Apr-11			
CR	Crismati	cri	f	3,2	Nov-04		Apr-09	
CR	Glori	glo	f	3,3	Feb-05			
CR	Leo	leo	m	3,4	Jul-06			
CR	Mamawoussia	mmw	f	4	aprox. 1990		Jan-11	
CR	Agustine	agu	m	4,1	Oct-06			
CR	Jone	jon	m	4,2	Nov-05		Jan-06	
CR	Doso	dso	f	4,3	Nov-08			
CR	Straight tail	str	f	5	aprox. 1995			
CR	Sabo	sab	m	5,1	May-03		Jan-11	Jan-11
CR	Fari	fri	m	5,2	Apr-05			
CR	Janet	jan	f	5,3	Oct-06		Sep-10	
CR	Delta	del	m	5,4	Nov-08			
CR	Babawoussia	bbw	m	1		Nov-05	Jan-09	
CR	David	dvi	m	2		Jan-03	Apr-11	
CR	Felix	fel	m	3		Jan-06	Apr-09	
CR	Lucas	luc	m	4		Dec-03		
CR	Wayo	way	m	5			Jan-09	
CR	Darwin	dwn	m	6		Feb-09		

Tab. 06.02. Age-classes: Definition of age classes used in previous studies compared to those used in this study (modified after Lowe 2014)

Classification used in previous publications (a)			Classification used in this publication	
Classification	Age (yr = years, mo = months)	Description	Classification	Description
Black Infant	0–7 months	Black coat, pink skin from birth to 5 months. Close association with mother.	Infant	Close association with mother and nursing. 0–2 years
Infant	7 mo–2 yr	Grey/ brown/ olive coat as in adults. Occasional nursing.		
Juvenile	Females: 2–4 years Males: 2–6 years	Not in association with mother for lengthy periods of time. Fully weaned. Larger than infant.	Juvenile	Not in association with mother for lengthy periods of time. Fully weaned. Larger than infant. 2 years - subadult stage
Subadult female	4–6 yr	Gradually grows to size of adult female. Red genital swellings.	Subadult female	Females are considered sub-adult on reaching menarche
Subadult male	6–10 yr	Larger than adult female. Lengthier mantle and shoulder hair. May spend time away from the troop.	Subadult male	Males are considered subadult when they are larger than adult females and grow lengthier mantle and shoulder hair. They may also spend time away from the troop.
Adult female	> 6 yr	Usually associated with offspring. Long, enlarged nipples and soft pale swellings. Nulliparous females considered adult if engage in consortship.	Adult female	Females are considered adults when they conceive their first infant. Nulliparous females also considered adult if they engage in consortship.
Adult male	> 10 yr	Long hair around neck and shoulder. Twice the size of adult female with large canines. Unbroken ischial callosities with a slightly raised centre line below tail.	Adult male	Males are considered adult when they have grown long hair around neck and shoulde and are twice the size of adult female with large canines. Adult males also have unbroken ischial callosities with a slightly raised centre line below tail.

(a) Ages are approximate

Tab. 06.03. Definitions of reproductive states

Reproductive state	Description
Menstrual cycle	From one menses to next, including swelling stages
Swelling stage 1	First stage of ano-genital swelling when inflation affects only top section
Swelling stage 2	Second stage of swelling, top and middle sections swollen
Swelling stage 3	Third stage of swelling. Top, middle and sides swollen. Includes day of ovulation, plus brief period of deflation
Pregnancy	Gestation, defined as lasting 6 months
Lactation	Nursing infant, with post-partum amenorrhea defined as lasting 1 year

Tab. 06.04. List of abbreviations

Category	Abbreviation	Description
Age-sex class	I	Infant
	J	Juvenile
	A	Adult
	F	Female
	M	Male
Reproductive state	S1	Swelling stage 1
	S2	Swelling stage 2
	S3	Swelling stage 3
	P	Pregnancy
	L	Lactation
Troop	CR	Crop-raiding troop Gamgam, near village of Gashaka
	WF	Wild-feeding troop Kwano, inside national park

RESULTS

Demography

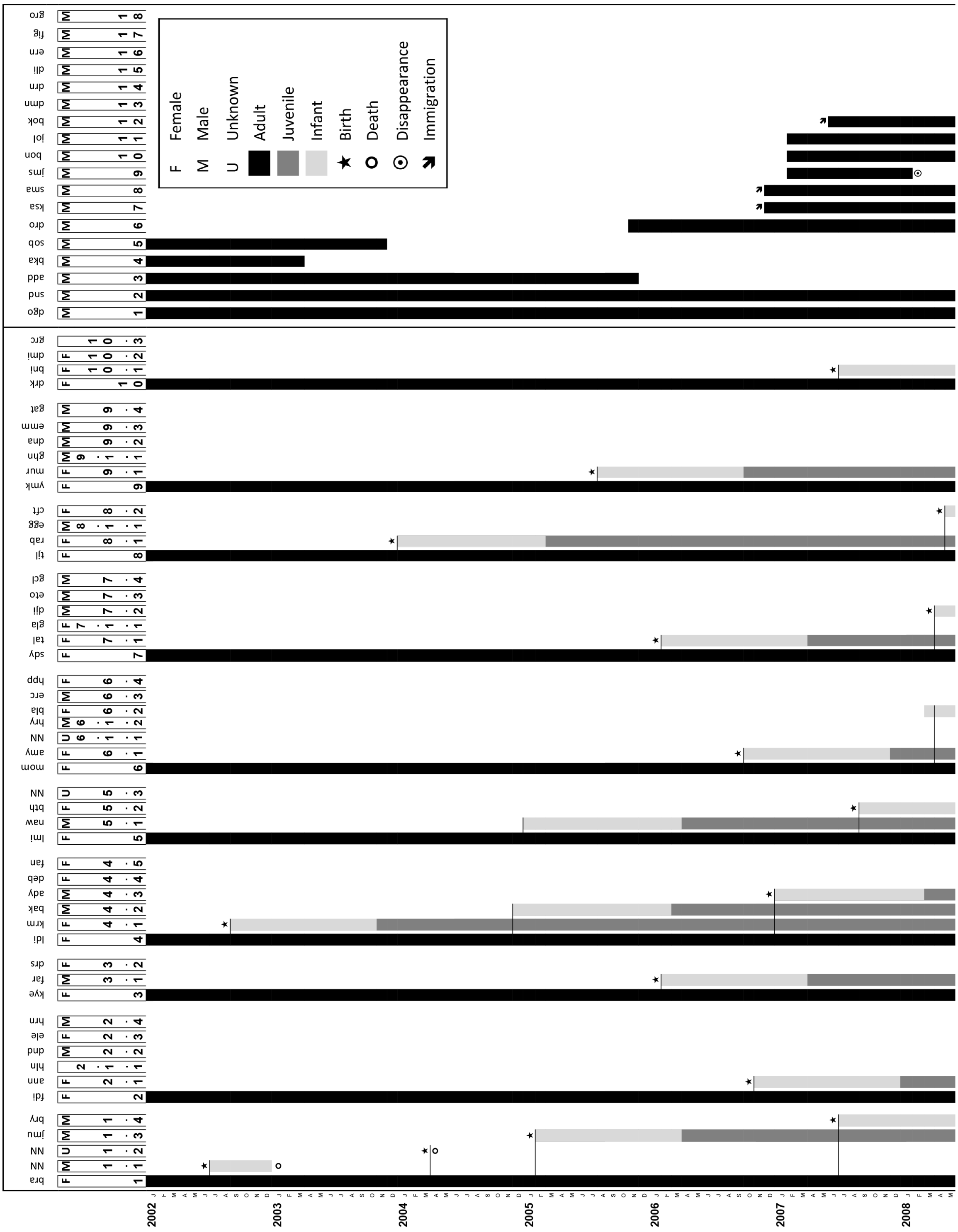
The membership composition of the two study troops is depicted in *Fig. 06.02*, illustrating the development, or at times disappearance, of matrilineal clans.

Troop sizes varied, depending on birth, death, emigration (natal dispersal) and immigration (from other troops). WF maintained a relatively stable size, oscillating between 25–37 animals. In contrast, CR membership decreased, from about 20 animals during 2007–2010 to only 10 members during 2011–2014 (*Fig. 06.03*). As discussed below, this is likely brought about by farmers killing the animals.

Age-sex composition are similar for CR and WF, but also contrasts in considerable ways (*Tab. 06.05*). In both troops, infants make up 9–10 % of group members, and there are fewer AM than AF. However, the juvenile sections differ substantially between CR (48 %) and WF (34 %). As a consequence, CR contain fewer adults overall (16 % AM, 27 % AM) compared to WF (21 % AM, 35 % AF).

These dissimilarities are partly reflected in the plotted survivorship curves that were based on the absolute counts. While CR troop, based on absolute counts, had a higher percentage of surviving group members up to 6 years of age (*Fig. 06.04a*), the corresponding survivorship curves were not significantly different (*Fig. 06.04b).*

As for sex-differential survivorship, with data for both troops pooled, there was likewise no statistically significant difference, albeit there was a trend that males die off faster than females (p = 0.08, *Fig. 06.05*).


F Female
M Male
U Unknown
Adult
Juvenile
Infant
Birth
Death
Disappearance
Immigration
2002
2003
2004
2005
2006
2007
2008
bra
NN
NN
jmu
bry
fdi
ann
hln
pnd
ele
hrn
kye
far
drs
ldi
krm
bak
ady
deb
fan
lmi
naw
bth
NN
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amy
NN
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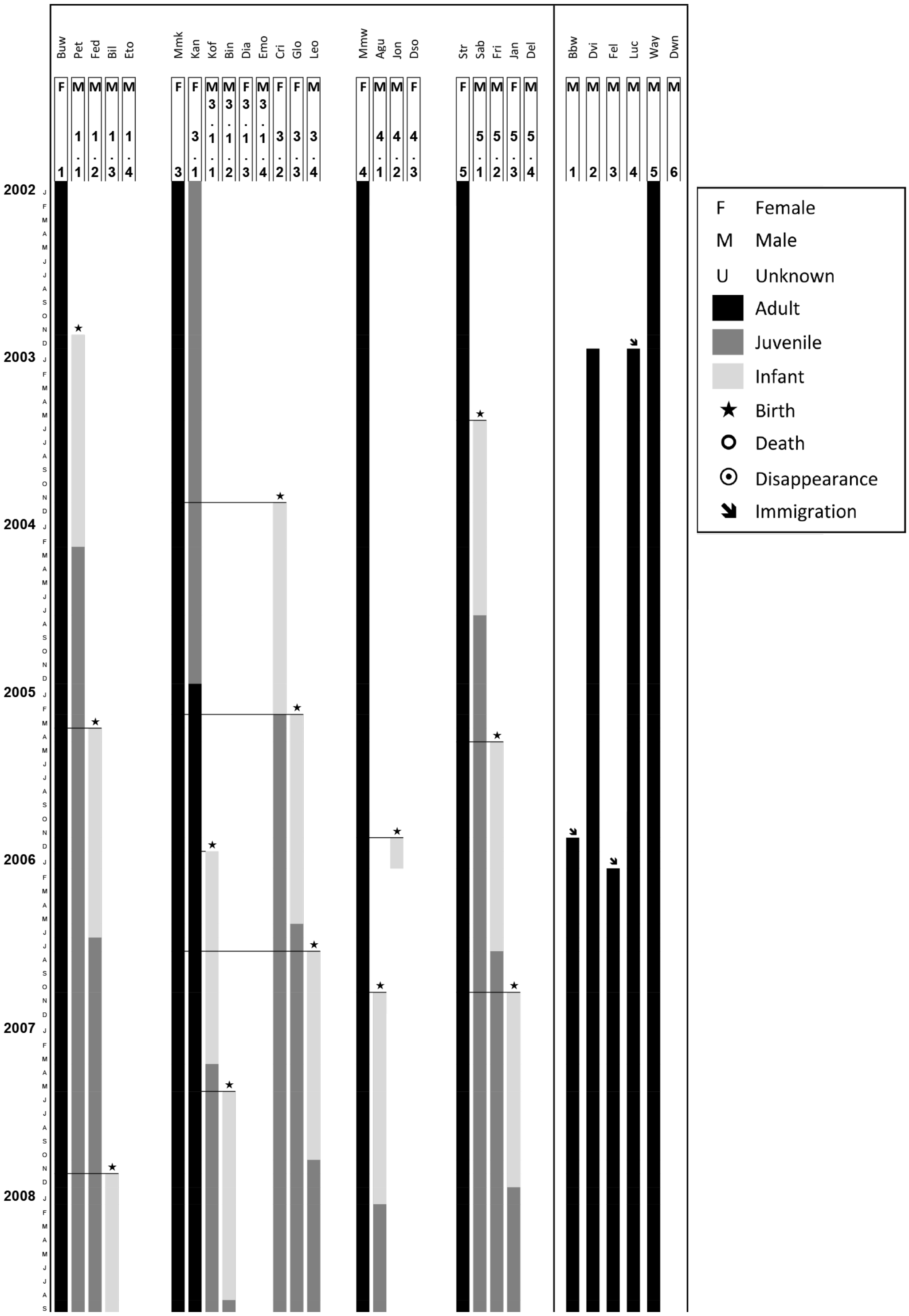
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Pet M 1.1
Fed M 1.2
Bil M 1.3
Eto M 1.4
Mmk F 3
Kan F 3.1
Kof M 3.1.1
Bin M 3.1.2
Dia F 3.1.3
Emo M 3.1.4
Cri F 3.2
Glo F 3.3
Leo M 3.4
Mmw F 4
Agu M 4.1
Jon M 4.2
Dso F 4.3
Str F 5
Sab M 5.1
Fri M 5.2
Jan F 5.3
Del M 5.4
Bbw M 1
Dvi M 2
Fel M 3
Luc M 4
Way M 5
Dwn M 6
2002
2003
2004
2005
2006
2007
2008
J F M A M J J A S O N D
F Female
M Male
U Unknown
Adult
Juvenile
Infant
Birth
Death
Disappearance
Immigration

(cont.)

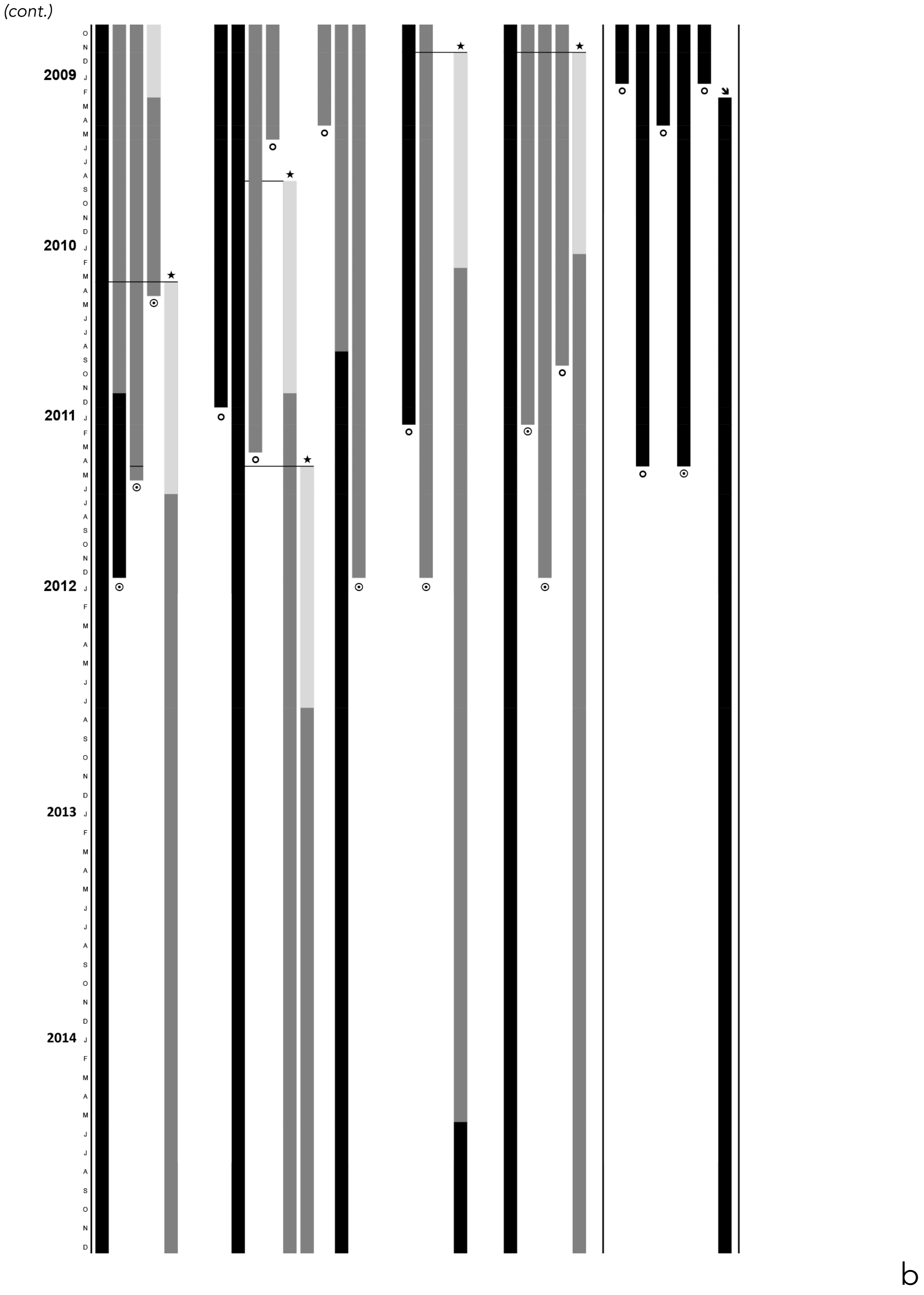


Fig. 06.02. Demographic development of two baboon study troops at Gashaka Gumti National Park (date of reference 10Mar15). (a) Wild-feeding troop Kwano. (b) Crop-raiding troop Gamgam

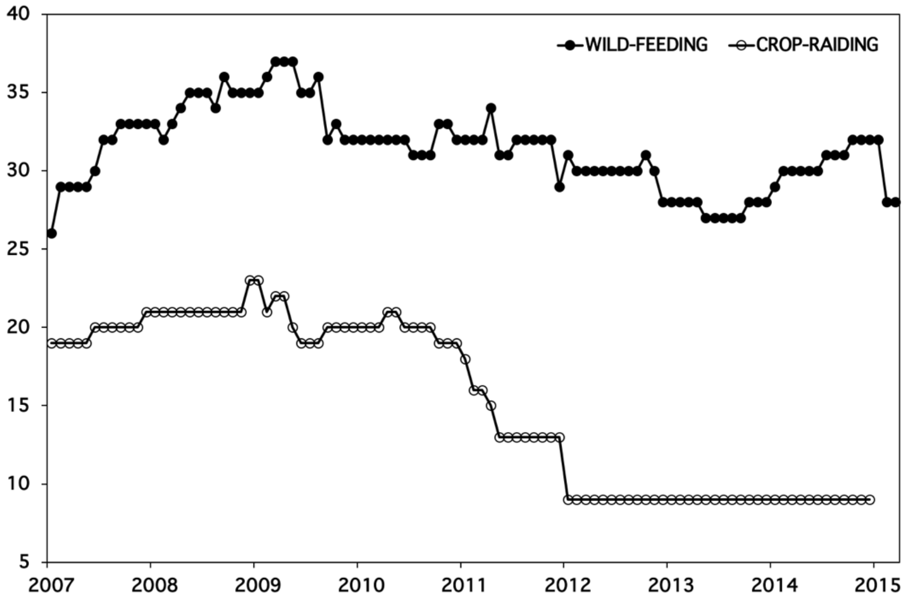


Fig. 06.03. Group size dynamics in two baboon study troops, 2007–2015. Records for 2002–2006 were incomplete and therefore not considered

Tab. 06.05. Age-sex class composition of two baboon study troops, 2007–2015. For each year, the mode of the number of animals in a certain class was considered. Date of reference: 10Mar15

Troop	Year	AM (%)	AF (%)	J (%)	I (%)
Wild-feeding	2007	28	31	25	16
	2008	24	30	33	12
	2009	25	31	36	8
	2010	19	32	39	10
	2011	19	31	44	6
	2012	16	39	39	6
	2013	21	43	32	4
	2014	20	43	27	10
	2015	18	36	29	18
	Average	21	35	34	10
	Range	18–28	30–43	25–44	4–18
Crop-raiding	2007	25	20	35	20
	2008	24	19	48	10
	2009	15	20	50	15
	2010	15	20	55	10
	2011	15	23	54	8
	2012	11	33	44	11
	2013	11	33	56	0
	2014	11	44	44	0
	Average	16	27	48	9
	Range	11–25	19–44	35–56	0–20

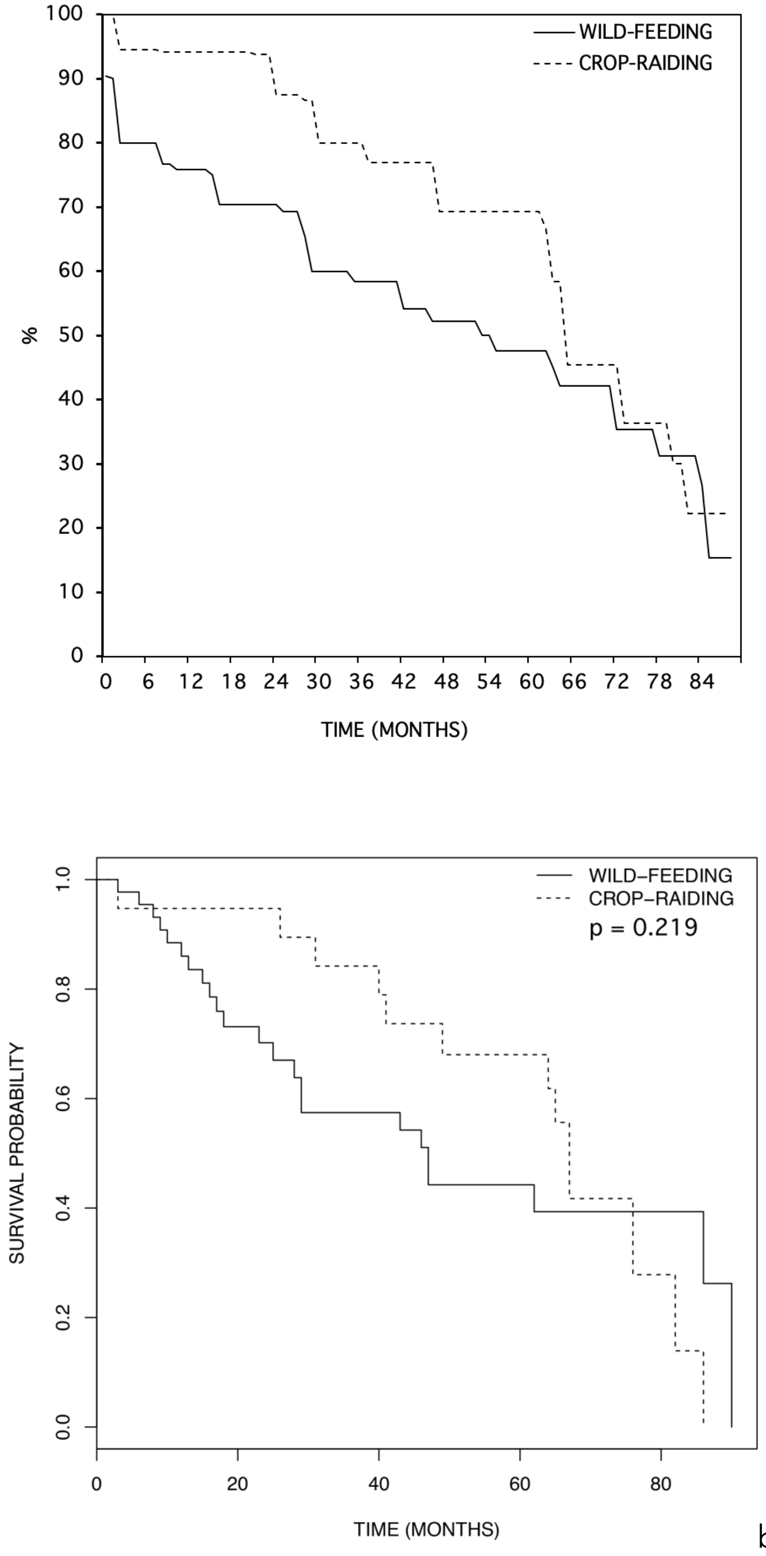


Fig. 06.04. Group-specific survivorship of baboons from birth till 90 months of age, born between 2004–2011, into wild-feeding troop Kwano (n = 32) and crop-raiding troop Gamgam (n = 18). (a) Survivorship curves with absolute counts. (b) Survivorship probability curves of baboons (Kaplan-Meier survival difference: $\chi^2(1) = 1.5$, rho = 1.5, p = 0.219 ns

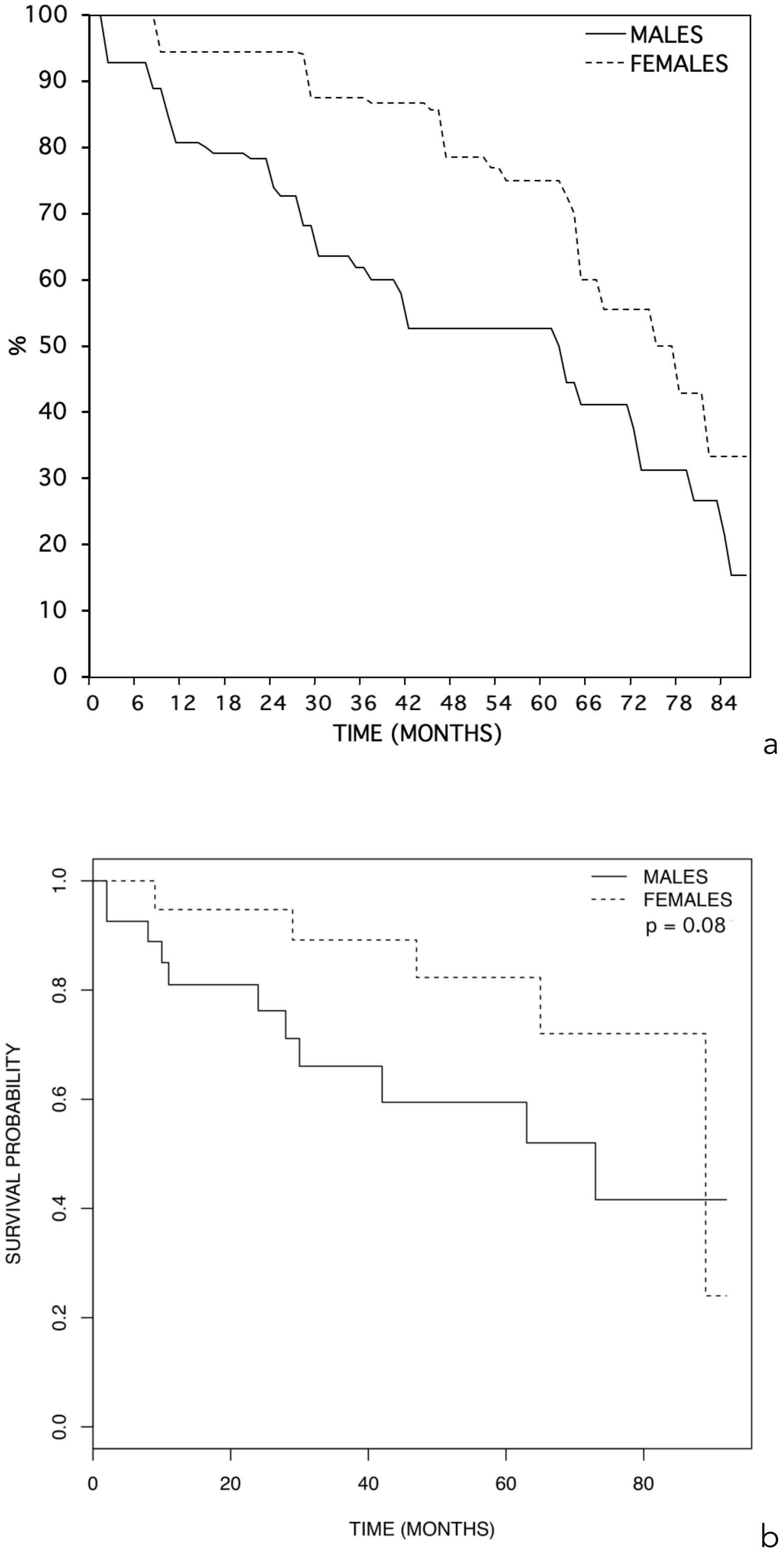


Fig. 06.05. Sex-differential survivorship of baboons from birth till 90 months of age according to sex (n = 27 males, n = 19 females). Combined data for wild-feeding troop Kwano and crop-raiding troop Gamgam, 2004–2011. (a) Survivorship curves with absolute counts. (b) Survivorship probability curves of baboons (Kaplan-Meier survival difference: $\chi^2(1) = 2.9$, rho = 1.5, p = 0.08 ns)

Menstrual Cycles

Once female baboons reach menarche and regular menstrual cyclicity kicks in, they produce sexual swellings around the time of ovulation. Our long-term records provide a wealth of information on inter- and intra-individual variation of reproductive parameters based on visually tracking the presence and absence of these swellings (*Tab. 06.06*).

Menstrual cycles of study females last on average 45 days (range: 24–73) (*Tab. 06.07*). Both troops show a similar spread of lengths, with a peak around 43 days, but CR registers the shortest cycles, whereas WF registers the longest (*Fig. 06.06*). However, this distribution does not translate into a statistically significant difference between troops ($p = 0.541$).

Similarly, when testing for a potential influence of the marked seasonality on the length of menstrual cycles (for both troops combined), again, no statistical difference was found ($p = 0.103$).

Tab. 06.06. Menstrual cycle lengths for females of two baboon study troops. Table displays the data in temporal sequence for individual females of wild-feeding troop Kwano and crop-raiding troop Gamgam. Cycle length was calculated from first day of observed S3 to the day before the next S3 was observed. Individual females' consecutive cycle length: numbers = length of cycle in days; (numbers) = assumed cycles in days with potentially substantial data errors, and therefore omitted from overall calculations; X = data missing for various lengths of time; PA = non-cycling period due to pregnancy and amenorrhea. These data and other reproductive parameters detailed in subsequent figures and tables are based on 12 Kwano females and 5 Gamgam females, 2004–2011

	Menstrual cycle length (days)																										
Wild-feeding	n	Mean	Median	Max	Min	SD	Individual females' sequences																				
Bera (F1)	2	45,5	46	49	42	4,9	(55)	(62)	X	PA	49	PA	X	(67)	X	(38)	X	(69)	42								
Fadi (F2)	3	48,7	45	59	42	9,1	45	(68)	(47)	(45)	(43)	X	(44)	(40)	X	(34)	PA	X	59	42	PA	X	(74)	(42)	PA		
Kaye (F3)	12	45,5	44	73	36	10,2	X	44	36	52	39	46	38	36	42	44	PA	52	(48)	X	(60)	73	44	X			
Ladi (F4)	2	46,5	47	49	44	3,5	44	PA	(52)	X	(36)	49	PA	X	(45)	X											
Karima (F4.1)	2	47,5	48	53	42	7,8	53	(47)	X	42	X	(40)	(45)	X													
Lami (F5)	3	43,3	44	46	40	3,1	X	PA	X	PA	X	44	X	40	46	PA	X										
Momi (F6)	4	40,5	40	47	35	5,5	47	(24)	(27)	X	35	X	PA	43	37	(44)	(44)	(39)	(49)	PA	X	(36)	X	(41)	(38)	PA	
Sadya (F7)	9	47,8	47	65	38	8,2	X	49	44	50,5	37,5	(42.5)	(51.5)	(40.5)	42	47	PA	(41)	41	54,5	64,5	PA	(40)	(38)	(42)	PA	
Tojali (F8)	5	46,2	47	59	34	11,6	35	X	PA	X	(60)	(42)	X	47	X	34	59	(50)	56	PA							
Rabi (F8.1)	3	37,0	35	42	34	4,4	(50)	(47)	34	(30)	(40)	X	35	42	(35)	(28)	(29)	PA									
Ymke (F9)	5	50,0	57	59	34	11,3	(43)	PA	X	(48)	(45)	X	34	59	57	X	(45)	(35)	58	PA	X	42	PA				
Dr. Kate (F10)	7	43,4	44	51	35	5,2	44	35	40	(31)	X	(39)	X	42	(91)	(28)	51	(48)	PA	(56)	(62)	(49)	48	44	X		
Crop-raiding																											
Budurwa (F1)	3	54,7	51	74	39	17,8	(49)	(45)	39	PA	74	51	(39)	X	PA												
Mamakane (F3)	5	49,0	49	53	45	2,7	PA	X	PA	X	48,5	X	45	50	52,5	49											
Kane (F3.1)	9	42,7	44	60	24	10,9	38	37,5	49,5	32	44	51	(43.5)	(34.5)	(29)	PA	X	PA	48	X	PA	24	(35)	60	(29.5)	(48.5)	PA
Glori (F3.3)	6	39,8	42	43	29	5,4	(48)	43	43	40	(27.5)	(46.5)	29	(69)	41,5	42,5	PA										
Straight Tail (F5)	5	44,9	45	56	37	7,3	45	PA	X	PA	(48)	X	56	46,5	PA	X	PA	X	40	37							

Tab. 06.07. Length of menstrual cycles in baboons comparing wild-feeding troop Kwano with crop-raiding troop Gamgam (Two Sample t-test: t(75) = 0.76, p = 0.451 ns) and across seasons (Two Sample t-test: t(50) = 1.66, p = 0.103 ns)

	Menstrual cycle length (days)					
	n	Mean	Median	Max	Min	SD
Troops compared						
Wild-feeding	51	45.2	44.0	73	34	8.2
		ns				
Crop-raiding	26	43.7	43.5	60	24	8.4
Troops combined	77	44.7	44.0	73	24	8.3
Annual variation						
Jan	9	46.7	42	73	35	13.6
Feb	6	41.1	41	49	34	4.6
Mar	14	46.0	44.5	59	36	6.8
Apr	9	42.5	44	51	24	7.5
May	10	47.5	48	65	34	8.9
Jun	4	47.0	45	60	38	9.4
Jul	5	40.2	40	45	35	4.1
Aug	4	46.6	50	51	36	7.4
Sep	3	47.0	49	52	40	6.2
Oct	3	38.7	37.5	47	32	7.3
Nov	6	39.5	41	45	29	6.0
Dec	4	51.9	52	58	46	5.2
Seasonality - 4-month peaks						
Wet season (Jul-Oct)	15	43.0	44	52	32	6.6
		ns				
Dry season (Dec-Mar)	33	46.0	44	73	34	9.0

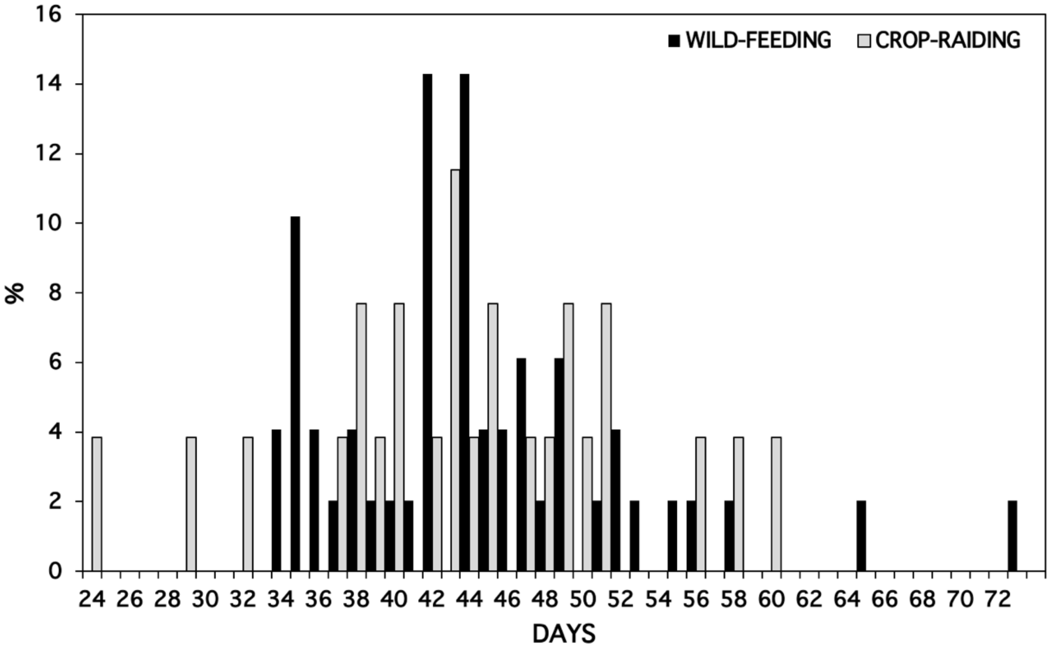


Fig. 06.06. Distribution of length of menstrual cycles in baboons of wild-feeding troop Kwano and crop-raiding troop Gamgam

Ano-genital Swellings

Swellings grow progressively larger until they reach maximum tumescence (S3), to then quickly deflate. Consecutive swellings recorded for study troop females are detailed in *Tab. 06.08*.

The time from when the swelling begins to show (S1) until its peak persistence (S3) represents about half of the total menstrual cycle length (20.8 days of 44.7 days = 47.5 %, range 7–40 days; *Tab. 06.09*). As for menstrual cycles, both troops show a similar length distribution, but CR again registers the shortest periods and WF the longest (*Fig. 06.08*). This spread translates into WF swellings being 1.2 days longer than those of CR females, a statistically significant difference (p = 0.019).

As for the length of the sexual swellings during the dry vs. the wet season, with data for the two troops combined, no seasonal effect was found (p = 0.382).

A separate analysis was conducted for the peak stage of swelling (S3) (*Tab. 06.10*). Again, no statistically significant difference was found between the troops (p = 0.296, *Tab 06.10, Tab 06.11*). However, as for seasonal differences, with records for both troops combined, there was a trend for-dry-season values to be shorter (by 2.5 days, p = 0.076).

Tab. 06.08. Ano-genital swelling lengths (stage S1–S3) for females of two baboon study troops. Table displays the data in temporal sequence for individual females of wild-feeding troop Kwano and crop-raiding troop Gamgam. Individual females' consecutive swelling length in days: numbers = length of swellings; (numbers) = length of assumed swellings with potentially substantial data errors, and therefore omitted from overall calculations; X = data missing for various lengths of time; PA = non-cycling period due to pregnancy and amenorrhea

	Ano-genital swelling length (S1–S3; days)																													
Wild-feeding	n	Mean	Median	Max	Min	SD	Individual females' sequences																							
Bera (F1)	4	25,0	26	40	8	15,0	35	PA	X	8	X	PA	X	40	(21)	X	17	X												
Fadi (F2)	7	22,6	23	27	18	3,1	X	18	X	X	21	24	PA	25	(19)	(22)	X	27	20	23	X	PA	(36)	X	(21)					
Kaye (F3)	9	24,1	23	33	10	7,0	26,5	(30)	29	10	18,5	(31.5)	(27.5)	(34.5)	X	PA	31	(21.5)	(28)	X	33	23	23	22,5	X	(21)	PA			
Ladi (F4)	5	18,6	18	28	10	8,3	26	PA	10	18	X	PA	28	X	(12)	(15)	(11)	PA	X	11	(14)									
Karima (F4.1)	4	21,9	21	27	18	4,4	(21)	18,5	24	27	X	(13)	(11)	X	18	(18)	PA													
Lami (F5)	2	19,0	19	22	16	4,2	X	16	PA	X	(21)	X	22	PA	X	(21)	(22)	X	(31)	PA										
Momi (F6)	11	23,0	24	30	18	3,9	(26)	29,5	23,5	21	27,5	(14.5)	X	PA	26	18	23,5	(18.5)	22	18	18,5	X	25	(24)	(18)	X	(17)	(10.5)	(15)	PA
Sadya (F7)	8	22,9	24	28	14	5,0	14	X	23	X	28	(25)	(29)	PA	(17)	X	23	25	28	P	X	PA	X	(21)	25	(20.5)	17	PA		
Tojali (F8)	3	23,3	23	25	22	1,5	PA	X	(24)	X	23	X	25	22	X	(28)	PA													
Rabi (F8.1)	2	21,8	22	22	22	0,4	(18)	(21.5)	(26.5)	X	(14.5)	(24.5)	22	21,5	PA															
Ymke (F9)	13	20,6	22	28	8	4,7	P	22	PA	X	25	X	19,5	21,5	23,5	21,5	22	18	17	27,5	X	8	PA	X	21,5	20,5	PA			
Dr. Kate (F10)	4	22,5	22	27	20	3,1	27	X	21	X	(17)	(26)	X	(29)	(23)	PA	X	(24)	X	(19)	(17)	22	PA	20	(14)	X	(9)			
Crop-raiding																														
Budurwa (F1)	6	24,6	23	35	16	7,5	(18)	19	15,5	22	PA	32	(27)	35	X	24	PA	X												
Mamakane (F3)	8	18,0	20	26	7	7,7	24	PA	24	PA	(12)	PA	(21.5)	7	X	10	(17.5)	X	25,5	26	(16.5)	X	15,5	12						
Kane (F3.1)	6	21,8	22	28	16	4,5	25	(28.5)	(27.5)	X	(23)	PA	18	X	PA	20,5	23	28	16	(29)	PA									
Glori (F3.3)	5	21,1	21	26	17	3,3	22	26	(27.5)	(23)	19,5	17	(21)	X	21	PA														
Mamawoussia (F4)	3	12,2	12	17	8	4,5	11,5	PA	17	PA	(11.5)	8																		
Straight Tail (F5)	6	19,5	20	24	16	2,9	PA	21	PA	24	20	PA	X	19	PA	X	16	17												

Tab. 06.09. Length of ano-genital swellings (stage S1–S3) in baboons of wild-feeding troop Kwano versus crop-raiding troop Gamgam (Two Sample t-test: t(106) = 2.39, p = 0.019*) and across seasons (Two Sample t-test: t(64) = -0.88, p = 0.382 ns)

	Ano-genital swelling length (S1–S3; days)					
	n	Mean	Median	Max	Min	SD
Troops compared						
Wild-feeding	72	22.3	22.5	40	8	5.9
		*				
Crop-raiding	36	19.3	19	35	7	6.3
Troops combined	108	20.8	21.5	40	7	6.0
Annual variation						
Jan	7	24.7	27	32	14	6.5
Feb	13	20.6	21	25	17	2.8
Mar	15	18.0	18	28	10	5.7
Apr	23	22.1	22.5	40	7	8.0
May	9	22.2	22	35	12	6.0
Jun	7	24.7	25.5	28	17	3.7
Jul	5	25.1	25	30	21	4.1
Aug	5	22.6	24	28	16	4.8
Sep	6	19.8	22	25	10	5.7
Oct	10	20.0	18	33	8	6.7
Nov	3	19.0	21	22	15	3.9
Dec	5	19.0	18.5	28	10	6.7
Seasonality - 4-month peaks						
Wet season peak (Jul-Oct)	26	21.4	22	33	8	5.8
		ns				
Dry season peak (Dec-Mar)	40	20.2	20	32	10	5.6

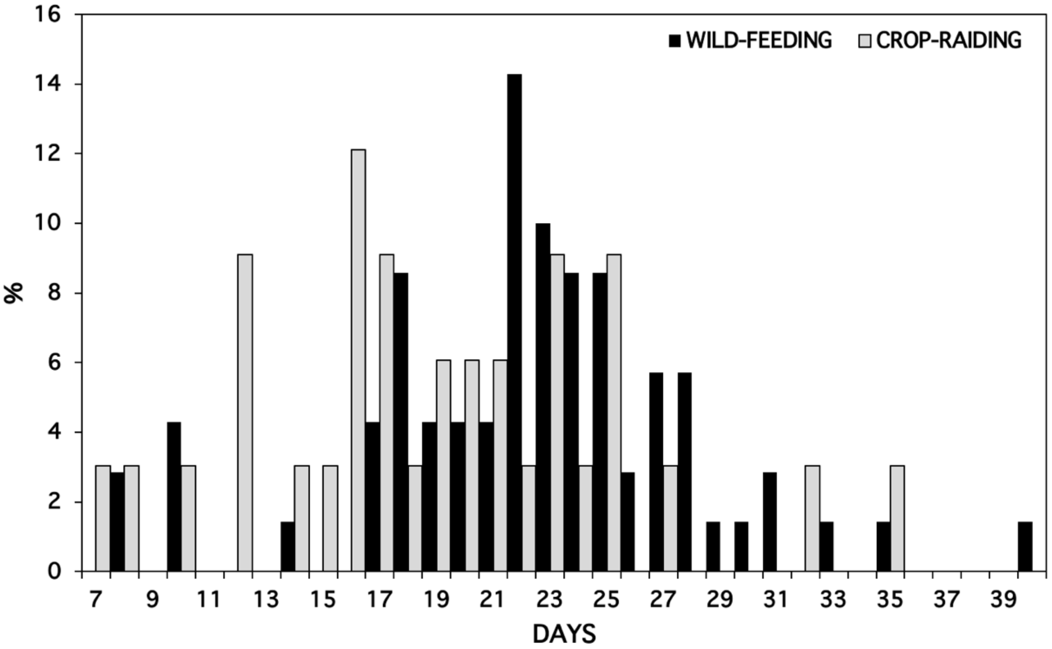


Fig. 06.08. Distribution of length of ano-genital swellings (stage S1-S3) in baboons of wild-feeding troop Kwano and crop-raiding troop Gamgam

Tab. 06.10. Ano-genital swelling peak lengths (S3) data for females of two baboon study troops. Tables display the data in temporal sequence for individual females of wild-feeding troop Kwano and crop-raiding troop Gamgam. Individual females' consecutive swelling peak in days: numbers = length of swelling peaks; (numbers) = length of assumed swelling peaks with potentially substantial data errors, and therefore omitted from overall calculations; X = data missing for various lengths of time; PA = non-cycling period due to pregnancy and amenorrhea

	Ano-genital swelling peak length (S3; days)						Individual females' sequences																									
Wild-feeding	n	Mean	Median	Max	Min	SD																										
Bera (F1)	2	4,0	4	6	2	2,8	PA	X	PA	X	2	X	PA	X	(4)	X	6	(9)	X													
Fadi (F2)	4	14,3	13	18	12	3,2	6	X	PA	X	13	12	18	X	PA	X																
Kaye (F3)	9	5,9	6	10	3	2,2	4,5	X	(7)	(12)	6	9,5	4,5	3,5	PA	8	(7.5)	X	3	X	7	X	(11)	(13)	5,5	PA	X					
Ladi (F4)	2	5,0	5	6	5	0,7	(7)	PA	X	PA	4,5	X	(8)	5,5	(5.5)	PA	(4)	X														
Karima (F4.1)	0	-	-	-	-	-	(2)	X	(8)	X	(9)																					
Lami (F5)	6	11,2	11	16	8	2,7	(3)	X	PA	7,5	PA	(8)	(20)	(15)	11	X	9,5	PA	(7.5)	(7.5)	12,5	X	11	(21)	15,5	PA						
Momi (F6)	5	9,5	12	13	4	4,8	5,5	3	13	X	4	X	(17)	(6)	(7)	X	PA	(8)	(6.5)	11,5	(11)	(11.5)	X	(10)	PA	(7)	(11)	X	(15)	(10.5)	PA	
Sadya (F7)	9	8,4	8	14	4	3,2	5	6	(13)	(16.5)	(14.5)	(6.5)	(9)	8	6	PA	4	X	7,5	10	9	P	14	PA	(6.5)	(6.5)	(11)	(8)	X	PA		
Tojali (F8)	6	9,7	10	14	6	3,1	X	(9)	5,5	7,5	(18.5)	(8)	X	9	14	12	10	PA														
Rabi (F8.1)	3	13,5	14	16	11	3,5	7	X	11	16																						
Ymke (F9)	8	11,6	11	17	7	3,7	(7)	X	7	PA	8,5	X	(8.5)	X	9	14	10	(10.5)	X	(11)	(10)	(10.5)	11	PA	X	17	16	PA				
Dr. Kate (F10)	3	4,0	4	4	4	0,0	(11)	11	4	(15)	X	(11)	(12)	X	(18)	(10)	PA	X	4	(10.5)	(9.5)	(8.5)	(9)	PA	X							
Crop-raiding																																
Budurwa (F1)	3	4,8	4	7	4	1,9	X	(11)	3,5	PA	7	4	(8)	X	PA	X																
Mamakane (F3)	3	10,5	11	12	9	2,1	PA	8	X	9	(7.5)	X	12	X	(9)	X																
Kane (F3.1)	6	9,9	8	16	6	4,5	(10)	13	14	(3.5)	X	15,5	X	PA	8	X	PA	6	(7)	(9.5)	6	X	PA									
Glori (F3.3)	7	7,3	8	12	2	3,9	(13.5)	9	11	(6.5)	4	(20.5)	2	9	6	11,5	PA															
Straight Tail (F5)	4	8,0	6	15	5	4,7	(8.5)	PA	X	(9)	PA	6	15	PA	X	5	6															

Tab. 06.11. Length of ano-genital swelling peak (stage S3) in baboons of wild-feeding troop Kwano with crop-raiding troop Gamgam (Two Sample t-test: t(64) = -1.05, p = 0.296 ns) and across seasons (Two Sample t-test: t(41) = 1.82, p = 0.076 ns)

	Ano-genital swelling peak length (S3; days)					
	n	Mean	Median	Max	Min	SD
Troops compared						
Wild-feeding	54	7.9	7.5	17	2	4.0
		ns				
Crop-raiding	23	8.4	8	16	2	3.8
Troops combined	77	8.0	7.5	17	2	3.9
Annual variation						
Jan	8	8.6	8	17	3	4.4
Feb	8	7.9	7	16	4	3.7
Mar	9	10.9	11.5	16	4	4.0
Apr	8	7.6	8	12	4	2.6
May	9	6.9	7	11	3	2.9
Jun	2	6.5	6.5	8	6	1.4
Jul	3	7.2	6	13	3	5.3
Aug	5	6.3	4.5	14	3	4.4
Sep	4	8.4	8.5	13	4	4.8
Oct	2	2.3	2	3	2	1.1
Nov	4	5.3	6	7	2	2.2
Dec	4	7.4	7	11	4	3.2
Seasonality - 4-month peaks						
Wet season (Jul-Oct)	14	6.5	5	14	2	4.5
		ns				
Dry season (Dec-Mar)	29	9.0	9	17	3	4.0

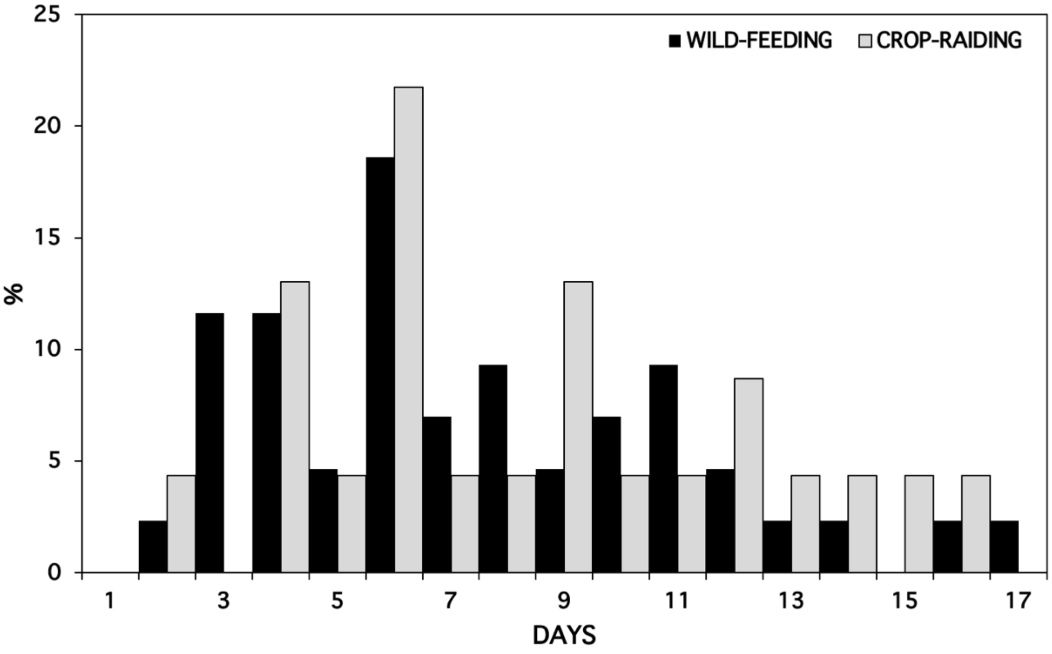


Fig. 06.09. Distribution of length of ano-genital swelling peak (stage S3) in baboons of wild-feeding troop Kwano and crop-raiding troop Gamgam

Menstrual Cyclicity and Parity

Cycling is interrupted from the beginning of a pregnancy and through the period of lactational amenorrhea (*Fig. 06.10*). Basic reproductive parameters were analysed for potential differences between nulliparous females and those that had already given birth. Accordingly, parous females have significantly longer cycles (mean 48 days) compared to those that have not yet given birth (mean 41 days, p = 0.018). However, parity does not affect the length of ano-genital swelling stages (*Tab. 06.12*, *Fig. 06.11*).

Fig. 06.10. Lactation: Females with nursing infants. Left: Fadi (F2) with 2-wk old Harrison (M2.5); right: Dr Kate (F10) with 7-mo old Grace (F10.3). (Photo: Adriana Lowe)

Tab. 06.12. Basic reproductive parameters in nulliparous and parous baboon females. Nulliparous = data for adult females before their first birth; parous = data for adult females after their first birth. Combined data for two study troops. Values for older females (that were already adults at the beginning of the study) not included in calculations. (Two Sample t-test: Menstrual cycles t(38) = -2.48; p = 0.018*; Ano-genital swellings (stage S1–S3) t(35) = -1.27, p = 0.211 ns; Ano-genital swelling peaks (stage S3) t(36) = 0.75, p = 0.460 ns)

	n	Mean	Median	Max	Min	SD
Menstrual cycles						
Nulliparous females	17	41.1	42	53	29	6.6
		*				
Parous females	23	47.8	48	65	24	9.5
Ano-genital swellings (stage S1–S3)						
Nulliparous females	13	21.6	22	27	16	3.7
		ns				
Parous females	24	23.6	23	33	11	4.8
Ano-genital swelling peaks (stage S3)						
Nulliparous females	14	9.6	10	16	2	4.3
		ns				
Parous females	24	8.7	8	18	2	3.6

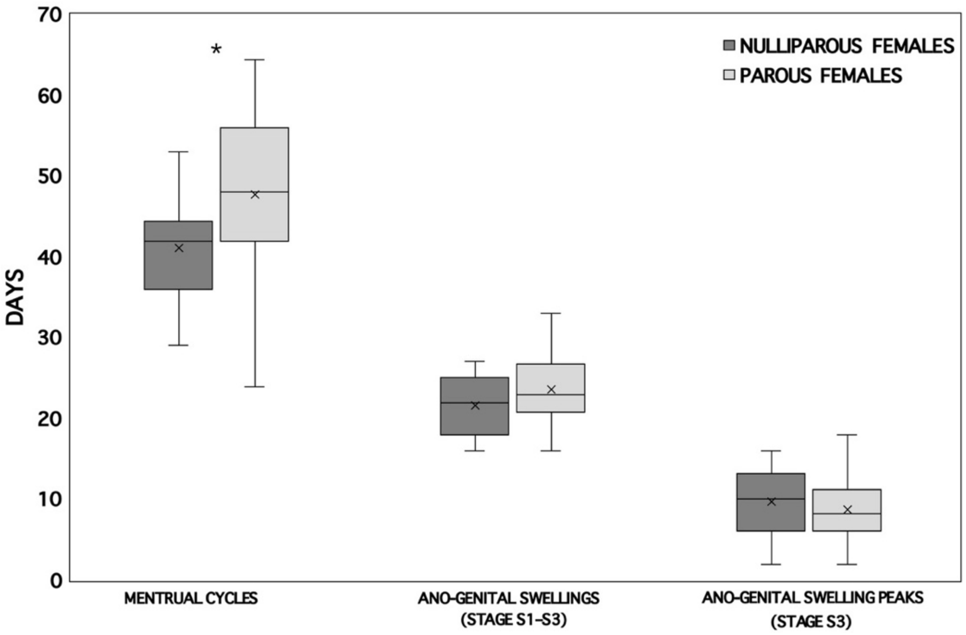


Fig. 06.11. Comparison of basic reproductive parameters in nulliparous and parous baboon females. Data from *Tab. 06.12*

Menstrual Cyclicity and Number of Troop Males

Given the hypothesis that females entice competition between males by advertising their fertility, the length of basic reproductive parameters was plotted against the number of adult males residing in a troop over the years of the study (*Fig. 06.12*). However, a significant positive correlation was only found for WF cycle length (p = 0.017) and for WF peak swelling lengths (p = 0.007).

Gestation, Lactational Amenorrhea and Inter-birth Intervals

Given the hypothesis that food regime may influence the length of major reproductive stages, the two troops were compared with respect to gestation, lactation and birth intervals.

As for females being pregnant, even experienced field assistants will initially fail to categorise them as such in the recording sheets – while they hardly ever failed to spot a pregnancy from three months onwards (*Fig. 06.13*). This mistake can, however, be retrospectively rectified through re-classification of a given female's reproductive state.

Average lengths of various major reproductive stages were as follows (*Tab. 06.13*): gestation 186 days, postpartum amenorrhea 347 days (1.0 years), inter-birth interval 896 days (2.5 years). After the loss of an infant, the residual postpartum amenorrhea was dramatically shortened to just 43 days, as was the birth interval (523 days = 1.4 years). This means, that whether or not females are mother to a dependent infant, they need about 1 1 / 2 years before conceiving again.

The troops did not significantly differ for gestation lengths (p = 0.863). However, WF females had significantly longer amenorrhea, both postpartum (p = 0.011) and after the loss of an infant (p = 0.024), and highly significant longer birth intervals (2.9 years for WF, compared to 1.8 years for CR, p < 0.001). That this trend was not echoed in birth intervals after the loss of an infant is likely an effect of the very small sample size of only 3 infant deaths.

Survival curves for the length of the postpartum amenorrhea confirm that CR females resume menstrual cyclicity much faster than WF females (p = 0.038, *Fig. 06.14*).

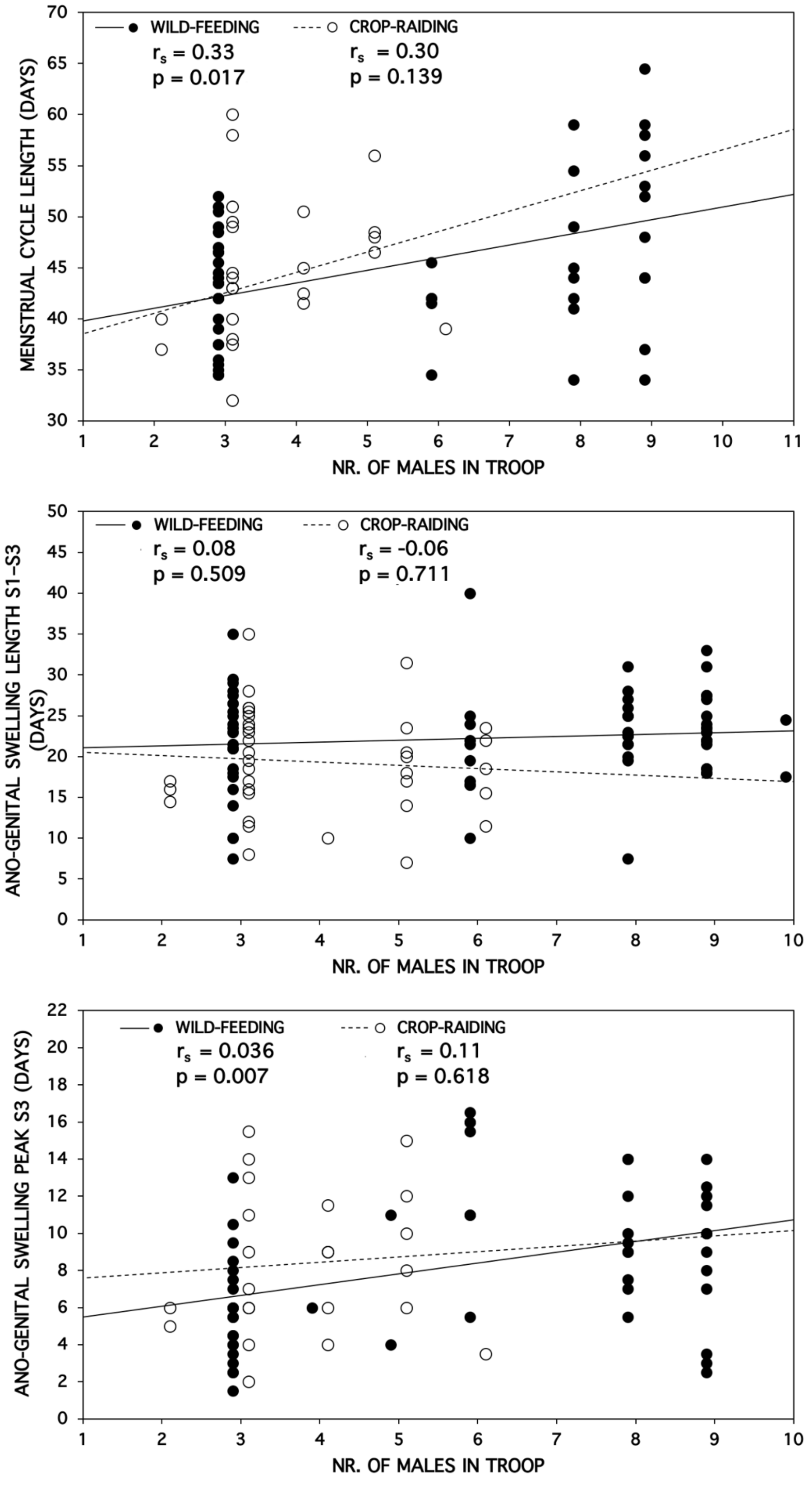


Fig. 06.12. Correlations between the number of males present and length of basic reproductive parameters of baboon females (a) Menstrual cycles (Spearman's rank order correlation: wild-feeding troop $r_s = 0.33$, $n = 51$, $p = 0.017$; crop-raiding troop $r_s = 0.30$, $n = 26$, $p = 0.139$). (b) Ano-genital swellings (stage S1–S3) (Spearman's rank order correlation: wild-feeding troop $r_s = 0.08$, $n = 72$, $p = 0.509$; crop-raiding troop $r_s = -0.06$, $n = 36$, $p = 0.711$). (c) Ano-genital swelling peak (stage S3) (Spearman's rank order correlation: wild-feeding troop $r_s = 0.036$, $n = 53$, $p = 0.007$; crop-raiding troop $r_s = 0.11$, $n = 23$, $p = 0.618$).

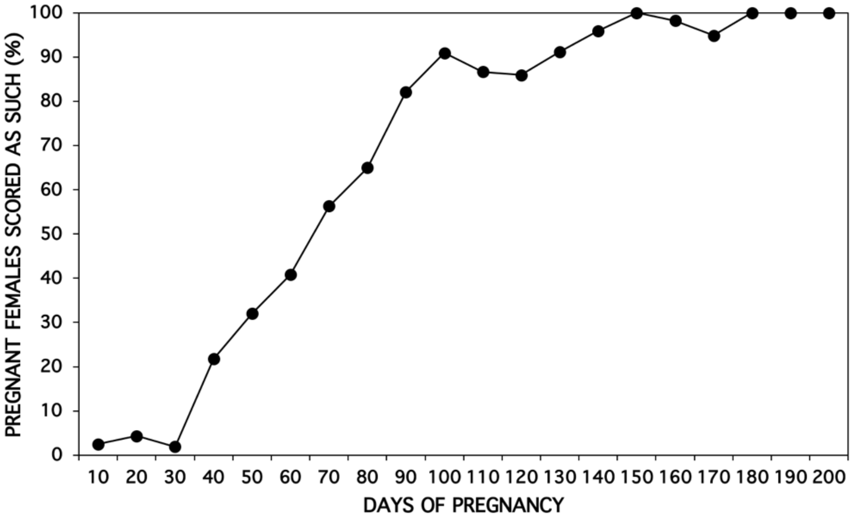


Fig. 06.13. Percentage of baboon females correctly scored as pregnant by field assistants, in relation to the progression of the pregnancies. Scores were derived post-hoc from data collection sheets and known dates of birth of infants born into wild-feeding troop Kwano (n = 12) and crop-raiding troop Gamgam (n = 8), 2004–2011

Tab. 06.13. Duration of important reproductive stages in baboons of wild-feeding troop Kwano versus crop-raiding troop Gamgam. Gestation (Two Sample t-test: t(18) = -0.17, p = 0.863 ns), postpartum amenorrhea (Two Sample t-test: t(18) = 2.84, p = 0.011*), post infant death amenorrhea (Two Sample t-test: t(1) = 26.37, p = 0.024*), inter-birth interval (Two Sample t-test: t(22) = 4.22, p < 0.001***) and inter-birth interval post infant death (Two Sample t-test: t(1) = 0.46, p = 0.726 ns)

		Days				
	n	Mean	Median	Max	Min	SD
Gestation length						
Wild-feeding	12	185.5	185	207	175	8.2
		ns				
Crop-raiding	8	187.4	183	255	126	36.7
Troops combined	20	186.3	184	255	126	23.1
Postpartum amenorrhea						
Wild-feeding	12	401.5	450	525	212	105.4
		*				
Crop-raiding	8	264.5	243	438	114	106.5
Troops combined	20	346.7	347	525	114	123.9
Post infant death amenorrhea						
Wild-feeding	2	54.3	54	55	54	1.1
		*				
Crop-raiding	1	20.0	20	20	20	-
Troops combined	3	42.8	53.5	55	20	19.8
Inter-birth interval						
Wild-feeding	14	1062.4	966.5	1582	686	256.9
		**				
Crop-raiding	10	663.9	608	981	459	178.4
Troops combined	24	896.3	899.5	1582	459	300.1
Inter-birth interval post infant death						
Wild-feeding	2	476.0	476	653	299	250.3
		ns				
Crop-raiding	1	616.5	616.5	617	617	-
Troops combined	3	522.8	616.5	653	299	194.7

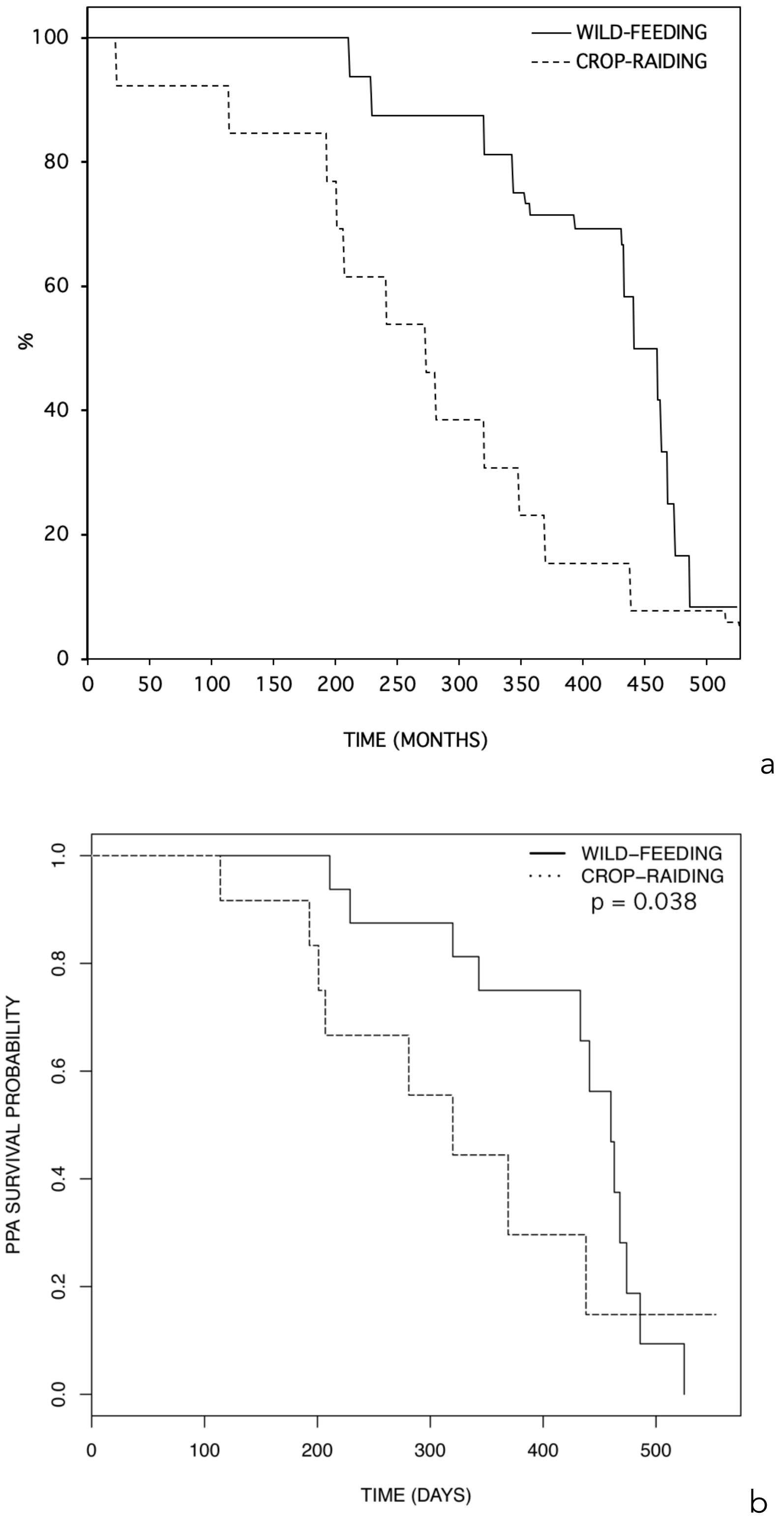


Fig. 06.14. Duration of post-partum amenorrhea in baboon females of wild-feeding troop Kwano (n = 12 births) compared to crop-raiding troop Gamgam (n = 8 births). (a) Survivorship curve with absolute counts. (b) Survivorship probability curves (Kaplan-Meier survival difference: $\chi^2(1) = 4.3$, rho = 1.5, p = 0.038*)

Reproductive Parameters and Environmental Factors

Finally, it was tested if the lengths of reproductive parameters co-varied with environmental factors (climatic seasonality, measured via rainfall; wild food availability, measured via fruit abundance).

Simple linear regressions revealed that neither the marked seasonality of rainfall nor that of fruit availability influenced menstrual cycle length (*Fig. 06.15*). This was true for both troops (*Fig. 06.16*).

However, the lengths of swellings displayed a slight seasonal pattern, with noticeable peaks in Jan and Jun–Jul (*Fig. 06.17*). In fact, in both troops, swelling lengths increased significantly with increasing rain (<u>WF</u> $p < 0.001$, <u>CR</u> $p = 0.048$; *Fig. 06.18a*), while this effect was not evident for fruit availability (*Fig. 06.18b*).

The same analysis for only the S3 swelling stage (*Fig. 06.19*) did not confirm the positive association with rainfall (*Fig. 06.20a*). However, S3 duration in the WF females increased significantly as a function of fruit abundance ($p = 0.005$), while no such effect was seen in CR troop (*Fig. 06.20b*).

In terms of the distribution of births across the year, there is no obvious annual pattern in either troop, despite higher frequencies in the second half of the year (*Fig. 06.21*). Similarly, there is no obvious pattern of the frequency of infant deaths, despite more infants passing away in WF troop during some months in the second half of the year (*Fig. 06.22*).

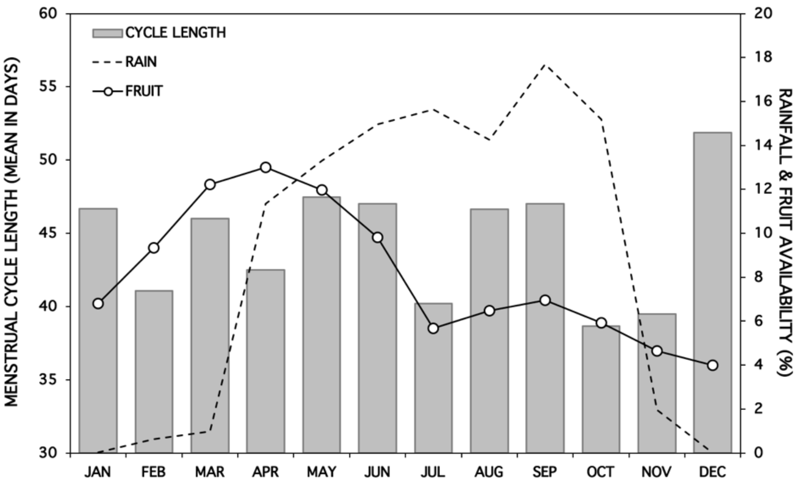


Fig. 06.15. Monthly menstrual cycle length (combined for females of two baboon study troops) in relation to environmental factors (monthly rainfall and fruit availability; 2004–2011)

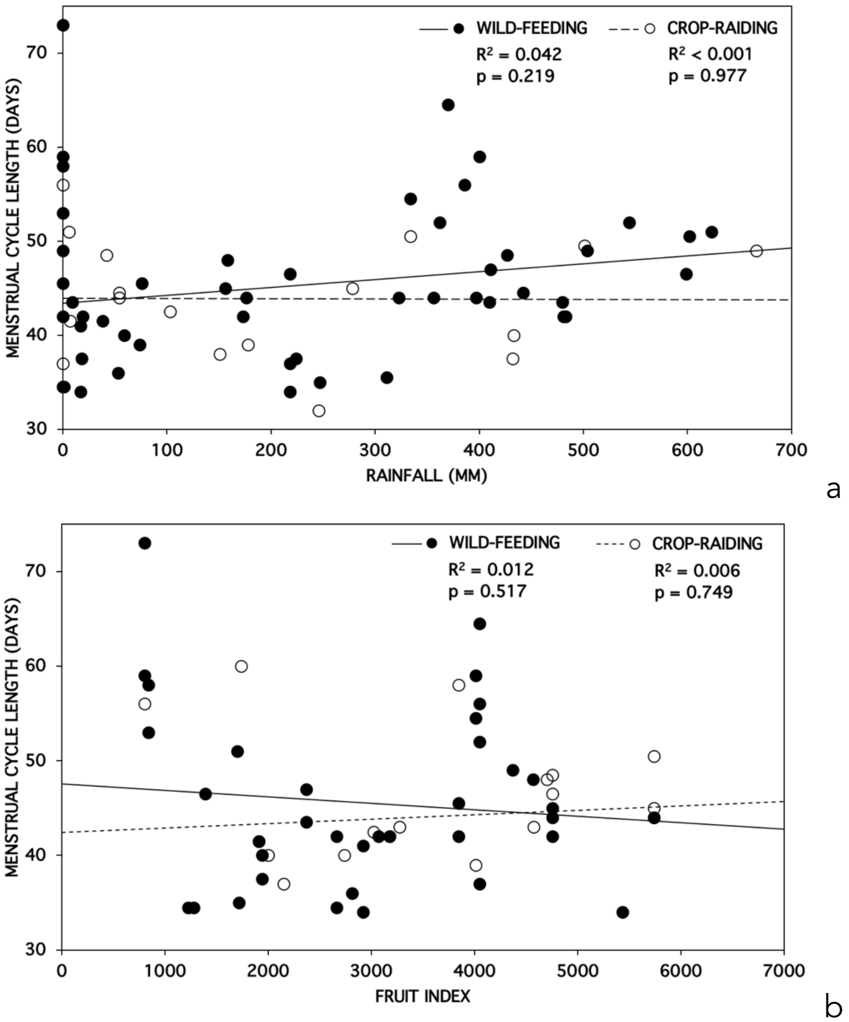


Fig. 06.16. Monthly menstrual cycle length as a function of environmental factors in baboons. (a) Length versus rainfall (single linear regression: wild-feeding troop F(1,48) = 2.081, p = 0.156 ns, R^2 = 0.042; crop-raiding troop: F(1,15) = 0.0008, p = 0.977 ns, $R^2 = 5.5e^{-05}$. (b) Length versus fruit availability (single linear regression: wild-feeding troop F(1,36) = 0.429, p = 0.517 ns, R^2 = 0.012 crop-raiding troop: F(1,16) = 0.007, p = 0.749 ns, R^2 = 0.006)

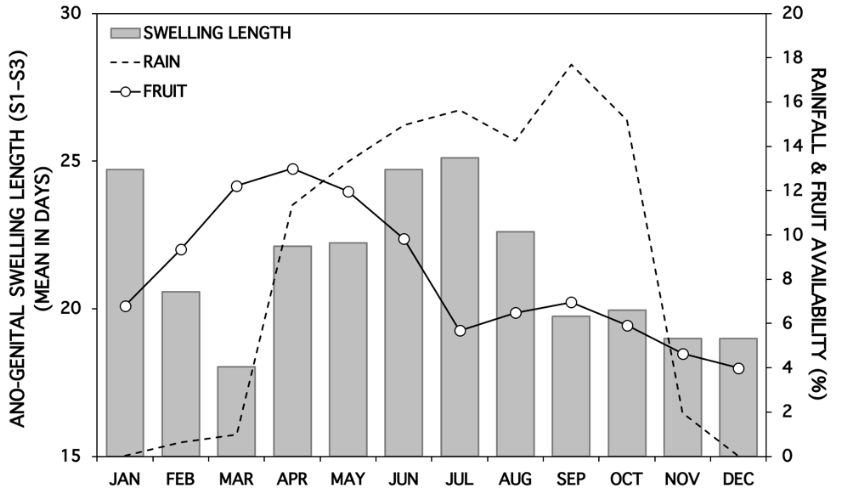


Fig. 06.17. Monthly length of ano-genital swellings (stage S1–S3, combined for females of two baboon study troops) in relation to environmental factors (monthly rainfall and fruit availability; 2004–2011)

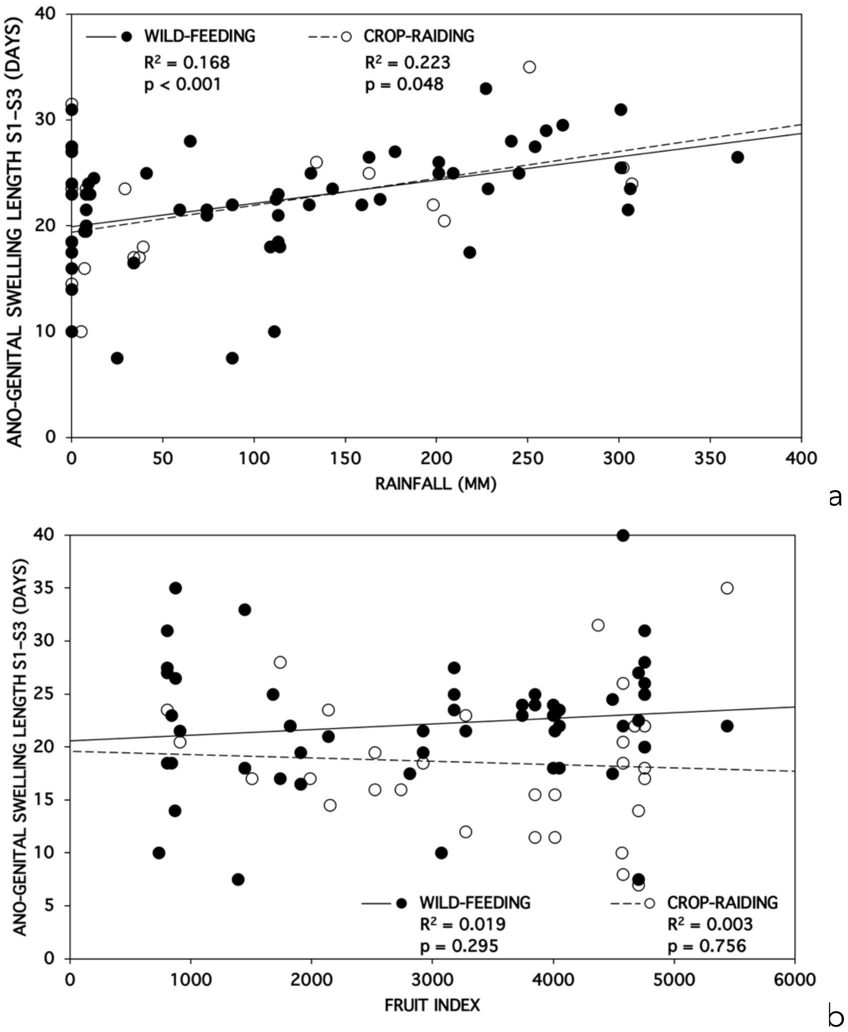


Fig. 06.18. Monthly length of ano-genital swellings (stage S1–S3) as a function of environmental factors in baboons. (a) Length versus rainfall (single linear regression: wild-feeding troop F(1,61) = 12.34, $p < 0.001$**, $R^2 = 0.168$; crop-raiding troop: F(1,16) = 4.603, $p = 0.048$*, $R^2 = 0.223$. (b) Length versus fruit availability (single linear regression: wild-feeding troop F(1,56) = 1.119, $p = 0.295$ ns, $R^2 = 0.019$ crop-raiding troop: F(1,29) = 0.099, $p = 0.756$ ns, $R^2 = 0.003$)

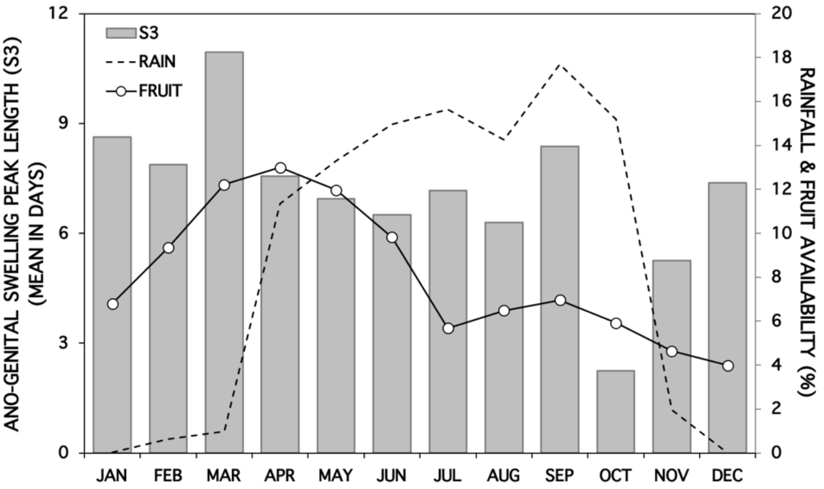
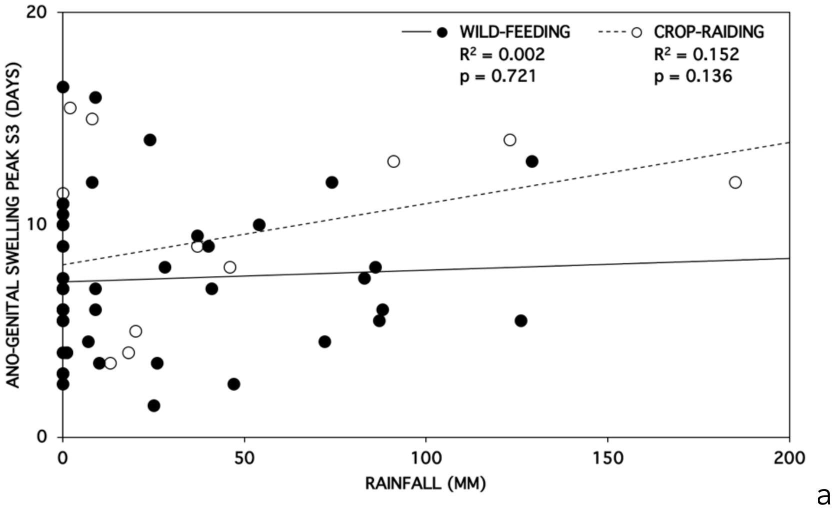


Fig. 06.19. Monthly length of ano-genital swelling peak (stage S3, combined for females of two baboon study troops) in relation to environmental factors (monthly rainfall and fruit availability; 2004–2011)



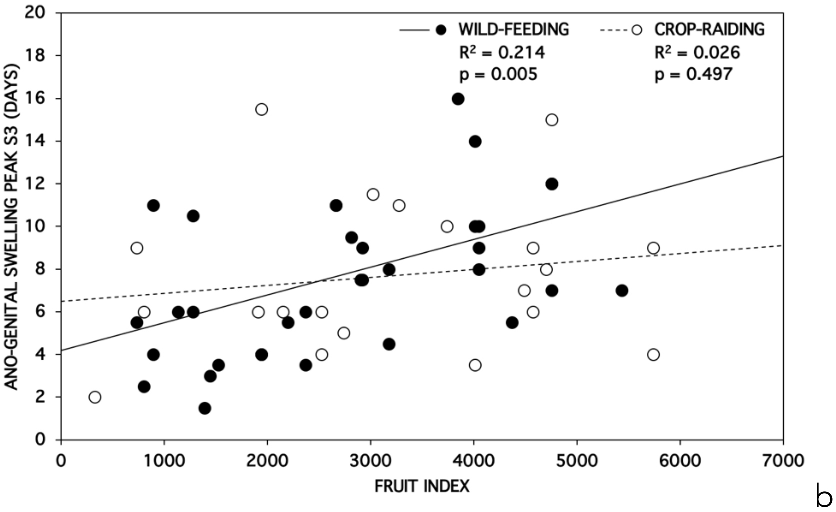


Fig. 06.20. Monthly length of ano-genital swelling peak (stage S3) as a function of environmental factors in baboons. (a) Length versus rainfall (single linear regression: wild-feeding troop F(1,40) = 0.129, p = 0.721 ns, R^2 = 0.002; crop-raiding troop: F(1,14) = 2.502, p = 0.136 ns, R^2 = 0.136. (b) Length versus fruit availability (single linear regression: wild-feeding troop F(1,33) = 8.975, p = 0.005**, R^2 = 0.214 crop-raiding troop: F(1,18) = 0.4811, p = 0.497 ns, R^2 = 0.026)

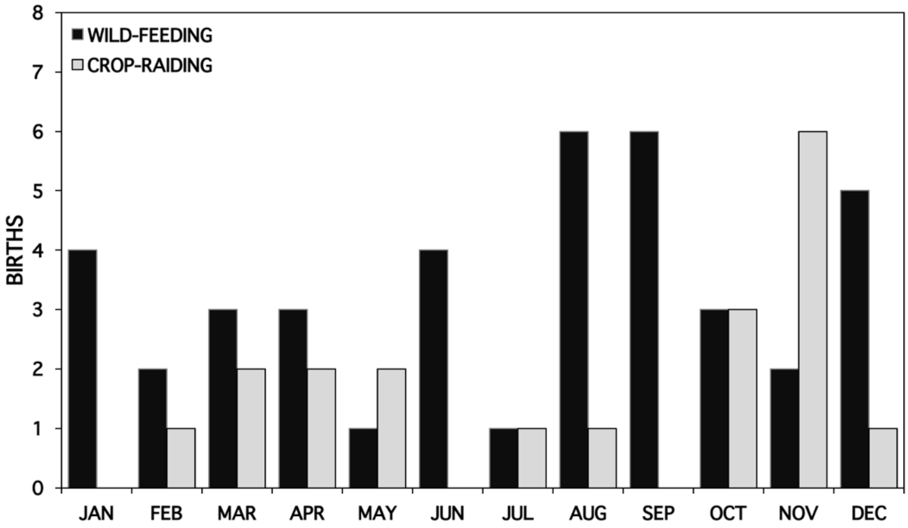


Fig. 06.21. Distribution of births across months (n = 59) in two study troops (2004–mid 2014)

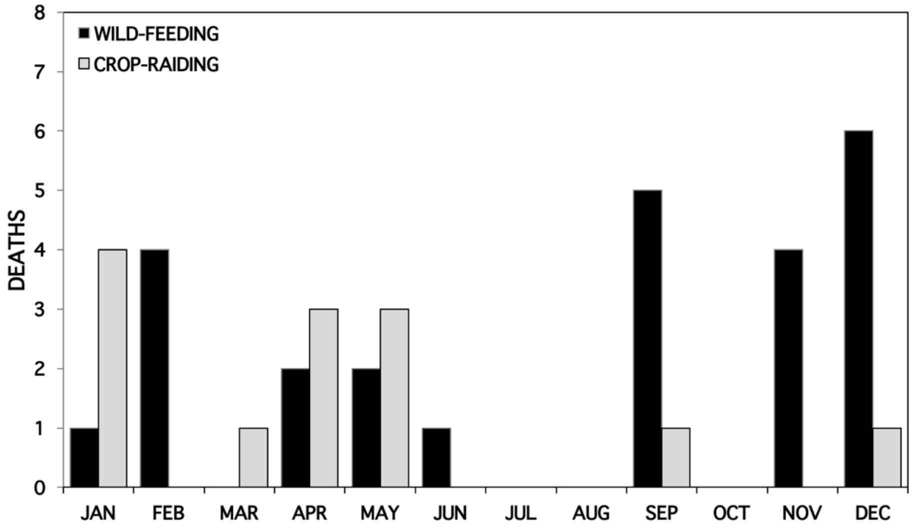


Fig. 06.22. Annual distribution of infant deaths (n = 38), in two study troops (2004–mid 2014)

DISCUSSION

Each day, more and more natural habitats are converted to alternative land uses, like farming. Thus, wild animals living in the surroundings are increasingly exposed to human produced crops which tend to be more palatable, digestible, energy-rich, and clumped within easily reachable areas (i.e. fields, plantations) (Hockings & McLennan 2012). For animals with access to such cultivated produces, a clear advantage is expected with regard to energy gains in comparison with those that feed solely on wild food sources. Nonetheless, exposure to anthropogenic habitats also comes with potentially lethal hazards like retaliation from farmers and exposure to human parasites and diseases (Drewe *et al*. 2012, Fehlmann *et al*. 2017).

As in the previous chapter, comparisons between the two Gashaka baboon study troops with very different foraging opportunities (wild-feeding versus crop-raiding) were analysed, this time in terms of the disparities in demographic and life-history traits that might be brought about by a diet enhanced with human cultivated crops.

The marked fluctuation between wet and dry season, constitutes an additional challenge for the baboon study troops which have to cope with periods of extreme dryness and periods when air humidity is above 90%. This study also considered how seasonality (i.e. rain and fruit availability) might interfere in baboon reproduction and whether crop-raiding can potentially minimise such effect.

Demographic Composition

WF troop always had more members than CR (cf. *Fig. 06.03*). This may seem counter-intuitive, as crop-raiding, theoretically, should increase reproductive rates and survival. However, a reduction in the spatial distribution and size of food-enhanced populations is known from elsewhere (Malik & Johnson 1994, Wheatley & Putra 1994). Contributing factors are increased risk of death while travel towards or being at locations where humans dwell, i.e. accidental contact with power lines, getting run over by vehicles, being attacked by dogs, drowning in ponds, tumbling to one's death from unfamiliar trees or rooftops, or falling victim to human-inflicted mortality via trapping, poisoning, stoning, shooting (Strum 1987, Rajpurohit & Sommer 1991).

Gashaka farmers see baboons as pests and are known to persecute CR individuals. Ironically, compared to other, often nocturnal, crop-raiders (e.g., red-river hog, bushbuck, cane rat, civet aardvark) or life-stock (cattle, sheep, goats, chickens), baboons may factually inflict less damage (Bennett & Ross 2011). Nevertheless, the monkeys are rated as the number one threat for crops (followed by porcupine, bush-fowl, warthog), not least, as baboons draw much attention because of their diurnal life-style, body size, vocalizations ("whao"-barks of males, Ey & Fischer 2011) and because researchers follow them. In any case, when research efforts were scaled down from about 2014, individuals started to disappear. By about 2016, all members of the troop were gone, most likely wiped out by farmers.

Survival Rates

Neglecting the fact that the "temptations" of crop-raiding ultimately doomed the CR troop, initial benefits of this foraging strategy can still be identified. Thus, CR has a higher preponderance of immature individuals (57 %) compared to WF (44 %) (cf. *Tab. 06.05*). Hence, immature CR baboons die off at reduced rates compared to WF youngsters. However, in terms of overall survivorship probability curves, no significant difference between the troops could be found (cf. *Fig. 06.04b).* In any case, by the time baboons reach adulthood this situation is most likely evened out as the baboons of the CR troop are targeted by retaliating farmers.

While female reproduction requires considerable investment of energy into gestation and lactation, male reproductive success is limited by access to fertile females (Trivers 1972). Evolutionary theory therefore predicts high levels of male-male competition with correspondingly high variance of reproductive success. As a consequence, males die off at greater rates than females – an effect that already kicks in at conception. This is, because males (foetuses, infants, juveniles, adults) will be less resilient against external stressors than females, given that selection will design fewer "repair" mechanisms for males in a situation where "the winner takes all" (review in Trivers 1985). These basic assumptions are confirmed by sex-differential survivorship curves for the study baboons (both troops combined), as males always tend to die off with greater likelihood (cf. *Fig. 06.05*).

Enhanced Food Speeds Up Female Reproduction

Improved access to food, particular such of higher quality, should allow females to reproduce faster (Harcourt 1989, Johnson 2006). This can be achieved if females need less time to become pregnant, by reducing gestation length and via earlier weaning of dependent offspring – ultimately reducing birth intervals. A comparison between CR and WF baboon females confirms some of these predictions, but not all.

Swellings may be a suitable tool to manipulate male behaviour to serve female reproductive strategies (Zinner *et al.* 2004), but they are energetically expensive (Anderson *et al.* 2006). It is therefore predicted that better nourished females have shorter ano-genital swelling periods. The same logic applies to menstrual cycle length, because the main variable that determines female reproduction is the length of the inter-birth interval (Gesquiere et al. 2018). Typically, once the lactational amenorrhea is over, females need several cycles to become pregnant again. Thus, because females can conceive only during ovulation, they would benefit from having shorter rather than longer menstrual cycles, in order to abbreviate the inter-birth interval as much as possible. Indeed, this interval is shortened in wild East African baboons, when females have more access to energy sources (ibid.).

However, given these predictions, the results for Gashaka baboons are, at best, in the right direction (cf. *Tab. 06.07, Tab. 06.09, Tab. 06.11*), but the differences are not statistically significant. Thus, CR menstrual cycles are 1.5 days shorter (a non-significant reduction by 3 %, compared to the mean for both troops) and their overall swelling length is 3 days shorter (a significant reduction by 14 %). Still, while the working hypothesis predicts shorter swellings, it may be that enhanced food actually enables females to extend the energetically costly, albeit crucial swelling phase. Moreover, in captive olive baboons, no relationship existed between total cycle length and daily food intake (Garcia *et al.* 2008). It therefore seems that the biology underlying the variation in sexual cycling duration is still not well understood (Gesquiere *et al.* 2018).

Another factor determining inter-birth intervals is the length of the pregnancy itself. However, compared to WF, CR pregnancies have virtually the same length. Although the data base is somewhat sketchy (and includes some rather unrealistic outliers), this confirms the idea that a life-history trait such as gestation is not very malleable by external factors.

In any case, post-natal periods are dramatically abridged in CR females. The post-partum amenorrhea is 396 days shorter (a significant reduction of 39 %), and the birth interval 398 days (a highly significant reduction of 44 %). Accordingly, the time between successive births is reduced by 1.1 years compared to WF – a substantial difference.

A previous study at Gashaka (Lodge 2012, Lodge *et al*. 2013) already referred to in *Ch. 05* combined nutritional analyses with the collection of faecal samples of females for hormone analyses. Results established that the energy intake of females living in WF troop was 50 % lower than that of CR females, and that WF females also had 50 % higher glucocorticoid levels and substantially higher progesterone levels. Thus, the previous Gashaka study does not support former findings that the stressful activity of crop-raiding with its associated human-wildlife conflict produces higher glucocorticoid metabolite levels (Ahlering *et al*. 2011, for African elephants). Instead, the Gashaka study concludes that effects of crop-raiding behaviour as acute stressors on glucocorticoid levels must be more than compensated for by the energetic benefits. Moreover, the study suggests that energetic stress and elevated progesterone levels in WF troop may be the cause of longer IBIs of WF troop. This suggestion is not in line with the common notion that improved energetic conditions cause higher ovarian hormone levels which equate to better ovarian function, thus indicating better condition and reproductive potential. Instead, it may be possible that elevated progesterone levels are inhibiting ovulation or fertilization, thus leading to longer periods of cycling prior to successful conception as detailed in the current study.

Operational Sex Ratio

The reduced inter-birth interval at CR also has consequences for the operational sex ratio, i.e. the number of fertile females relative to adult males, which is a measure of how intense sexual competition is (Kvarnemo & Ahnesjo 1996). At first glance, based on proportions, there is no difference between troops in the ratios of adult females to adult males, with CR's being (27 % / 16 % =) 1.7, the same as WF's (35 % / 21 % =) 1.7 (cf. *Tab. 06.05*). However, it needs to be taken into account that CR females will be pregnant or lactating for a much greater proportion of time, thus reducing the availability of fertile mating partners for males. As a consequence, it can be expected stiffer male-male competition in CR – a prediction that could be followed up by comparing rates of male-male aggression in the two troops.

Overall, however, there was little evidence that the number of adult males that compete for females affected female behaviour. Thus, a significant positive correlation with an increased number of adult males was only found for WF cycle length (p = 0.017) and for WF peak swelling lengths (p = 0.007) (cf. *Fig. 06.12*). A lack of corresponding evidence for CR troop might reflect a lower amount of data (n menstrual cycle length: WF 51, CR 26; n swelling length WF 72, CR 36).

Thus, the hypothesis that females invest more time in trying to entice male-male competition, if they have "more choice", will need to be investigated further through careful analyses at the level of inter-individual interactions.

Menstrual Cyclicity and Parity

The data on basic reproductive parameters were analysed for potential differences between nulliparous females and those that had already given birth (cf. *Fig. 06.11*). While nulliparous females had significantly shorter menstrual cycles, there is no significant difference for swelling lengths. There isn't yet enough data on copulations or the likelihood of conception, but it seems that young females at least increase their proceptivity. This assumption is based in the fact that swellings cover 52 % of nulliparous cycle days, compared to only 49 % of cycle days of parous females.

Other studies confirm the idea that young females are less attractive and therefore increase their proceptivity. For example, in langur monkeys (*Semnopithecus entellus*) who do not display swellings, menstrual cycles do not differ in length between nulliparous and parous females, while the ovulatory phase (during which females solicit sex), is longer (Sommer *et al.* 1992). Reduced attractivity of nulliparous females for males along with extended swelling phases in first swellings has also been found in semi-free ranging mandrills as well as Tonkean (*Macaca tonkeana*), Barbary (*Macaca sylvanus*) and lion-tailed (*Macaca silenus*) macaques (references in Setchell *et al.* 2004). Nevertheless, in captive olive baboons, female age was not associated with menstrual cycle length (Rigaill *et al.* 2013).

Lack of Seasonality in Reproductive Parameters

The potential influence of environmental factors was investigated, in particular rainfall and availability of wild fruit, on reproductive parameters of the study baboons. However, despite the dramatically seasonal climate, i.e. several months without rain followed by heavy downpours, there was hardly any detectable effect.

The lengths of menstrual cycles and swelling periods did not differ between the wet and the dry season (cf. *Tab. 06.07*, *Tab. 06.09*, *Tab. 06.11*). Looking at the data on a month-to-month basis revealed that amount of monthly rain did not influence menstrual cycle length or peak swelling length, although overall swelling length (S1–S3) in CR as well as WF was positively – and significantly – correlated with increased precipitation (cf. *Fig. 06.15–05.20*). Perhaps, a more humid environment allows females to reduce the metabolic costs of building up the swellings, which depend on water retention.

Seasonal fluctuation of wild fruit availability did likewise not alter the duration of cycles or swellings – except that maximum swelling length in WF increased significantly, if more fruit was available (cf. *Fig. 06.15–06.20*).

The latter finding is in line with endocrinological explorations of the two study troops (MacLarnon *et al.* 2015). Over numerous years, faecal glucocorticoid (fGC) levels of CR and WF females were measured and scrutinized against the potential influence of ecological correlates (i.e. climate, food availability). The results suggest that WF females experience both thermoregulatory and nutritional stress, while CR experience only thermoregulatory stress. This difference may reflect nutritional stress-buffering in CR females – which, in turn, explains that CR female swelling length are not affected by fluctuations in wild fruit abundance.

The "net" outcome of these rather minimal seasonal effects is a lack of seasonality in terms of infants being born or dying (cf. *Fig. 06.21*, *Fig. 06.22*) – these events occur during rainless months as well as during the wettest months. The finding is somewhat unusual, because for many other primate species living in similar equatorial habitats, seasonal peaks in reproduction are linked to rainfall. These patterns are hypothesized to minimize energetic stress on the female or infant by aligning gestation, lactation or weaning with optimal food availability (references in di Bitetti & Janson 2000, Emery Thompson 2016). In any case, the Gashaka baboons support the statement of Alberts *et al*. (2005) that "among savannah-dwelling primates there are only two exceptions to the rule of seasonal reproduction: humans and baboons" (p. 157).

Food enhancement can mitigate such seasonal constraints. Thus, Indian langurs living in a very seasonal environment nevertheless reproduce year-round because local people provision them (Sommer & Rajpurohit 1989). Similarly, for the crop-raiding Gashaka baboons, it can be associated to the mitigating effect of their enhanced diet.

However, WF females experience thermoregulatory as well as nutritional stress, with swelling lengths affected by both rainfall and fruit abundance. Yet, this does not translate into birth seasonality (cf. Fig. 06.21) – a finding, for which currently there is no explanation.

In any case, given that baboons elsewhere, even in highly seasonal habitats, show little or no seasonal reproduction (Alberts *et al*. 2005, Altmann *et al*. 2010), these data are additional testimony to the extraordinary adaptability of this type of primate.

CHAPTER 07

OUTLOOK.

ENABLING RESEARCH AND CONSERVATION AT A BIODIVERSITY HOTSPOT

Research and Conservation: The Dual Capacity of Longitudinal Data Collection

The collection of longitudinal information at a field site (cf. Clutton-Brock & Sheldon 2010, Kappeler *et al.* 2012, Robbins 2010) embodies two important perspectives. The first is scientific and explicit, in that such data lead to academic publications. However, while long-term data sets may spurn the immediate production of research papers, they also function as a repository of background information that may aid future researchers or form part of extensive collaborative efforts. The second is applied and implicit. Because, apart from the academic exercise, field work can play an important role in the future preservation of the locale under study. Areas with ongoing long-term field projects are known to suffer less habitat disturbance than other protected areas and have higher wildlife densities (e.g., Wrangham & Ross 2008; Campbell *et al.* 2011; cf. also Tranquilli *et al.* 2014, a review stimulated by the first author's field work at Gashaka). Long-term projects also tend to provide employment opportunities in their vicinity because they usually operate in areas with little prospects for employment (cf. e.g., Kappeler *et al.* 2012).

The final chapter of this thesis will exemplify these two perspectives, by, on the one hand, detailing research that has built on the data collection described in this thesis, and on the other hand, by describing the conservation challenges the field site at Gashaka is facing, and how the Gashaka Primate Project has played a role in mitigating these threats.

Synthesising Plant and Animal Phenology

The following will provide examples that detail how the multi-facetted investigations at the Gashaka field site – i.e. data on climate, plant phenology, animal gregariousness – can contribute to answer more complex research questions.

The first two examples refer to the chimpanzees of the Kwano community (*Ch. 04*). A paper entitled "Till the last drop. Honey-gathering in Nigerian chimpanzees" (Sommer *et al.* 2012 – with GJ being a co-author) synthesised data to better understand the dynamics of how chimpanzees exploit bee nests. Various chimpanzee populations are known to target beehives to obtain honey, often with the help of wooden tools. At Kwano, chimpanzees use sturdy digging sticks and more slender probes, sometimes successively as a tool set, to access honey from subterranean and tree-dwelling colonies of stingless bees and honeybees. However, little is known about how honey abundance in tropical habitats fluctuates with season and how chimpanzees response to this. The long-term data compiled on monthly proportions of flowering trees and vines (*Ch. 03*) were used as a proxy for honey production, assuming that colonies hoarded more honey at the peak of the flowering season. During these periods, chimpanzees of the Kwano community abandoned more tools at individual beehives. One might assume that the increased number of tools reflected an increase in foraging day group sizes in that more chimpanzees were present when a hive was targeted. However, data on day groups (*Ch. 04*) allowed us to rule out such a correlation. Instead, individual apes used more probes during a given honey gathering event – presumably because dipping remained worthwhile for longer. Chimpanzees thus adjust the manufacture of tools to honey abundance, reflecting that the sugary fluid is a sought-after resource.

Another paper entitled "Sustained myrmecophagy in Nigerian chimpanzees: Preferred or fallback food?" (Sommer *et al.* 2016 – with GJ being a co-author) likewise focussed on how the Kwano chimpanzees obtain resources from colonies of social insects. At some sites across Africa, chimpanzees consume army ants, often aided by plant tools, although consumption frequencies vary greatly. Other populations do not eat these insects at all, despite apparent abundance. The relative importance of this type of myrmecophagy for chimpanzee diet therefore remains unclear. The research investigated for the Kwano chimpanzee community if army ants constitute a preferred food or a fallback resource, given that these insects are consumed here much more frequently than elsewhere. Again, the paper used long-term records on temporal variation of climate and availability of fruit (*Ch. 03*) – the preferred food of chimpanzees –, and compared that information to rates of recovered army ant dipping wands and army ant remains in faeces. The results showed that, despite strict seasonality of rainfall and fruit abundance, myrmecophagy does not negatively correlate with fruit availability. Instead, army ant eating is sustained year-round at high levels, with 44 % of faeces containing remains. Admittedly, to exclude a role as fallback food, the crucial test question is not whether army ant consumption is constant. Instead, one needs to ascertain whether harvests of these insects go up when consumption of preferred foods goes down. While there were no direct data for this, sizes of night groups (*Ch. 04*) served as a proxy for the level of food competition between individual chimpanzees. Accordingly, night groups are expected to become smaller when fruits as the preferred food are less abundant. Such a significant negative correlation was indeed found, while myrmecophagy did not increase. The results contradict the fallback hypothesis and support the hypothesis that ants are a preferred food. Nevertheless, compared to fruit, ant-meals can normally provide only negligible amounts of nutrients. At Gashaka, however, nutritional yield may be significant, given that ant-dipping sessions provide on average 13 mg of dry weight to a chimpanzee (Allon *et al.* 2012). The species exclusively eaten here, *Dorylus rubellus,* might be particularly aggressive, thus resulting in greater harvesting success than elsewhere. Army ants may hence serve as a diet supplement or complement in terms of macro- or micronutrients.

These examples illustrate that, despite an increasing tendency to "mathematize" research, solid natural history information is still required to serve as the baseline to construct statistical models. Thus, "old-fashioned" field research like the one exemplified in this thesis, will continue to play an important role in research about primate socioecology. That recognition is also exemplified by a review paper on the Gashaka baboons which illustrates how investigations into the phenology of plants (*Ch. 03*) and non-primate ecology (*Ch. 02*) can been fruitfully linked with studies of primate socioecology (*Ch. 05*, *06*).

The paper entitled "Antelope Predation by Nigerian Forest Baboons: Ecological and Behavioural Correlates" (Sommer *et al.* 2016, with GJ being a co-author) again relied to a large extent on data compiled in/for this thesis. Thus, over a 16-yr period, baboons of the Kwano and Gamgam study troops, were found to have killed 10 antelopes – 7 bushbucks and 3 red-flanked duikers, all infants. Controlling for observation effort, this translates into a frequency of one predation per troop every 3.3 months – far lower than elsewhere in Africa. Moreover, the Kwano-Gamgam area is only the second study site with predation records for bushbuck and the only one for red-flanked duiker. The atypical prey as well as the rarity of eating mammalian meat probably reflects the difficulty of acquiring prey animals when vegetation cover is dense – a feature quite different from most other baboon study sites. Baboons at Kwano-Gamgam may therefore be restricted to predation on still-lying "parked" infants that are opportunistically encountered – instead of actively "hunting" or "searching for" prey. Although duiker and bushbuck are spotted throughout the year in the study area, predation is highly seasonal. It occurs mainly during the early rainy season (Apr–Jun), coinciding with a lambing season of the two prey species. During this time, the savannah is blanketed by very tall grass (*Ch. 03*), providing much better cover than forests, where visibility is less compromised during the rains. This could explain why killings in closed forest were overrepresented, while those in woodland were considerably underrepresented – despite the fact that the reverse was true for sightings of adult bushbuck and red-flanked duiker. Grouping patterns of potential prey may also influence, which species fall victim to baboons and which do not. Piglets would seem like an obvious target, but might be hard to catch as they always travel with adults that are likely to defend them. As detailed in *Ch. 02*, red river hogs and giant forest hog move about in groups of 4–5 animals, with a maximum of 13. Infants of other antelopes may also be protected because they travel with adults. Thus, buffalo groups average 6 animals, with a maximum of 12, and those of waterbuck 3 animals, with a maximum of 8. Bushbuck and duiker, on the other hand, will often travel alone – and mothers park their babies in dense plant cover, risking, that baboons may stumble upon them.

Such analyses of baboon-prey interaction may seem straight-forward. Nevertheless, one needs to stress again how physically and logistically challenging mammal surveys in often-closed habitat are, with considerably restricted visibility, i.e. forest mixed with patches of savannah blanketed by tall grass for much of the year. A single researcher would be hard pressed to obtain the necessary back-ground data – a fact that once more stresses the importance of constructing long-term data sets.

Anthropogenic Disturbances

The 20th and 21st century have been seeing a steady loss of natural forests (e.g., Hansen *et al.* 2013, Laurance *et al.* 2014) which increasingly threatens the survival of more than half of all primate species (e.g., Chapman *et al*. 2017). Within this tide, GGNP is one of the last refuges in West Africa for wild fauna and flora (Oates *et al.* 2004). Still, this haven of biodiversity is likewise under increasing pressure from anthropogenic activity, many of which exert even greater dynamics in other African wildernesses (Cowlishaw & Dunbar 2000, Ammann *et al*. 2003, Arcus Foundation 2014).

At GGNP, a combination of anthropogenic fires and overgrazing constitutes the greatest hazard, as it leads to erosion (Adanu *et al.* 2011). To extend cattle pasture grounds and stimulate sprouting of new vegetation, grass is burned at the advent of the dry season (*Fig. 07.01a*). However, such burning selects for fire-resistant grasses that are hardly palatable to cattle, thus being counterproductive to the goals for which the fire-regime was originally designed. Moreover, nutrients are blown away and lost, and as the soil becomes compacted. Therefore, even fire-resistant savannah-trees find it difficult to rejuvenate. Cattle grazing, mostly by pastoralist Fulani, reduce the vegetation cover still further (*Fig.07.01b*). Cows trod a zigzag of tracks into the hills, creating perfect channels for rainwater to rush down. A chain of erosion is thus set in motion, ultimately causing whole hillsides to collapse in spectacular gullies – as has happened widely across the Mambilla Plateau adjacent to GGNP.

The succession of erosion – burning, grazing, washing-off of top-soil – affects not only the landscape outside the reserve, as thousands of heads of cattle are kept by Fulani clans in a handful of partly legal enclaves in the highlands of the southern Gashaka sector (Bennett & Ross 2011). More cattle are intermittently brought across the border from Cameroon. The enclaves were carved out when GGNP was created, around settlements that had evolved in the 1960s after Fulani migrated with their herds into the park's cool highlands to reduce tsetse fly bites and thus infection by sleeping sickness. The idea was to negotiate re-settlement outside the park boundaries at a later stage, but this never happened. The human population in the enclaves is now around 5,000 people.

In the park's surrounding, poaching is rampant (*Fig.07.01c*), and most areas have been shot empty of large mammals. Hunters, often coming from across the Cameroonian border, are increasingly targeting the reserve itself (Hughes *et al.* 2011). Conservationists have at times floated the idea that a Muslim taboo against eating, e.g., pork and primate meat would reduce hunting. However, this is wishful thinking, as Muslim hunters sell their haram meat to non-Muslim customers (Nyanganji *et al.* 2011).

Thus, human impact within the park is considerable – a shocking realisation to all those who thought that national parks are indeed sanctuaries of nature. Many areas in and around the enclaves in particular have lost more than a quarter of their vegetation cover between 1988–2000, as satellite-generated maps reveal (Gumnior 2008) (*Fig.07.02)*.

Fig.02.03. Conservation challenges in Gashaka Gumti National Park. (a) Seasonal burning of woodland-savannah during the dry season (02Feb05). (b) Overgrazing by Fulani herdsmen (08Jan12). (c) Hunting for bushmeat (poachers with colobus monkeys, after being arrested by rangers; 12Dec12). (Photos: © GPP, Volker Sommer [a], GGNP [b], GPP [c])

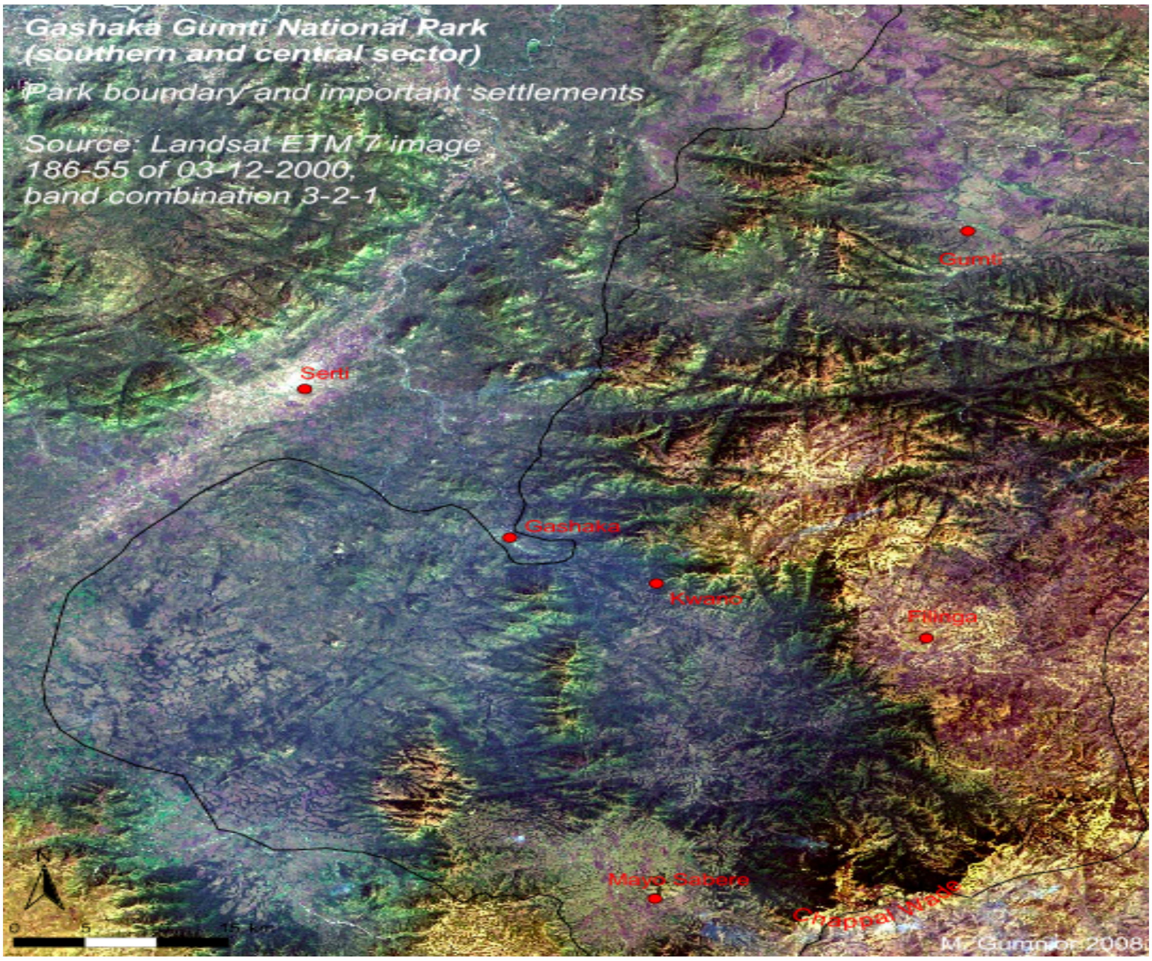


Fig. 07.02. Remote sensing scene of Gashaka Gumti National Park, with border indicated by thin black line. Note deforested areas, particularly in the south of the park on the Mambila Plateau and in the east across the border in Cameroon (© GPP)

However, new threats have emerged since about 2015. Increasingly, an invasive herb (*Chromolaena odorata*, the "devil weed") is strangling and outcompeting native savannah grasses (Borokini 2011). Artisanal mining for blue semi-precious gemstones such as amethysts takes place in the buffer zone of the Mambilla plateau where shanty towns have sprung up – a destructive development that is soon likely to spill over into the park (Ahmed & Oruonye 2016). There is also the threat that the River Donga, which has tributaries in GGNP, might soon be dammed near its source (Harris 2017). Impoverished migrants have moved from far-away places to colonize the park's buffer zone, with little means of survival other than targeting natural resources. Several illegal settlements have encroached well beyond the park boundary. All this drives the illegal construction of tracks for motorbikes and four-wheeled vehicles and thus adds to the further perforation of the park's landscape.

Until lately, outright logging was a relatively small problem – although many parts in the parks wider vicinity had been denuded by the local timber industry. However, since mid 2016, hundreds of trucks crawl through Taraba State, with crews paying cash to locals who have (mostly illegally) cut and hoarded thousands upon thousands of logs at make-shift depots along the roadsides. Locally called the "rose-wood-craze", the tree mostly targeted is *Pterocarpus erinaceus*, the African rosewood. Its hard wood is exported to China, where it is known as "kosso", to manufacture decorative luxuriant furniture (Gaworecki 2016). The tree, native to the vulnerable savannah ecosystems of West Africa, has thus become an increasingly threatened species. Already, the over-harvesting of kosso is causing visible desertification in Taraba State, including the drying up of rivers, while also depriving local communities of a resource traditionally used for fuel, construction, musical instruments, traditional medicine and animal fodder (Koutsioni *et al.* 2011).

These disturbing human activities are likely to continue and increase in scale. Even if they do not lead to outright destruction of the fine-tuned ecosystem, they would slowly alter its structure. For example, if large mammals are increasingly hunted out, they would cease to disperse certain types of large seeds, which would shift the forest composition towards trees with smaller seeds (Fleming & Estrada 1986).

Having said all this, it has to be pointed out that the relatively remote Gamgam-Kwano study area (cf. *Fig.02.05*) has until recently remained quite safe from destruction – not least, because of outreach activities of the Gashaka Primate Project, achieved in close cooperation with the National Park Service. This perspective of longitudinal data collection shall be exemplified in the concluding part of this thesis.

Conservation Activities

The GPP research trajectory originally focused on the behavioural ecology of non-human primates (Sommer & Ross 2011). Since founded by Volker Sommer in the year 2000, the project has highlighted the importance to save the remote wilderness of Gashaka-Kwano from destruction by human activities. To this end, GPP strategically stressed the precarious state of the park's flagship species, the Nigeria-Cameroon chimpanzee, of whom probably less than 2500 or so individuals survive (Morgan *et al.* 2011).

Various campaigns – several of them coordinated and executed by me –recruited sponsors in Europe and Africa to engage in joint protection measures (see also *Ch. 02*). These include providing educational, economic and infrastructural benefits to local communities and national park rangers in this secluded highland region.

The design of GPP centres on the use of research outcomes to support conservation activities tied to capacity building, particularly among the 214 or so rangers employed by the park. Various public and media engagement activities were used to create awareness about the importance of conserving the iconic but fragile Gashaka Gumti wilderness and its chimpanzee flagship species, and to raise funds. These events included dozens of interviews and articles in international media outlets, as well as talks in 7 European countries plus interviews and programmes for Nigerian radio and TV stations. Of particular importance were contacts with Julius-Berger-Nigeria (JBN), one of the largest construction companies in sub-Saharan Africa, with headquarters in Abuja, Nigeria and Wiesbaden, Germany, which included talks to senior management, employees and their families as well as in the company-run school, which often led to JBN employees visiting the park itself.

One of GPP's first major projects was the demarcation of the vast reserve's hitherto "invisible" border – constructing beacons and motorable tracks to improve ranger patrolling. Funded by Chester Zoo, UK, the initial demarcation of 225 km of park border was completed in late 2009; a programme of on-going maintenance and improvement since then has included its extension in 2013 to the grazing enclaves that lie within the park. Marking the boundaries has removed legal ambiguities and significantly improved law enforcement, providing incontrovertible evidence to support charges against illegal activities such as poaching, cattle grazing and forest cutting. Hundreds of such incidents have since been reported to Taraba State's law enforcement agencies

From 2008, park management has been further improved by an additional GPP initiative facilitating the identification of hotspots in which unusual rates of plant cover loss require special attention. Supported by funding from the US Fish and Wildlife Service, GPP began a satellite-based vegetation mapping of the park as part of its biodiversity research (Gumnior & Sommer 2012). Several park officials were trained to interpret remote sensing imagery through GIS, and a set of related soft- and hardware was handed over to the park management in 2010.

The research project also initiated seed programmes to improve park ranger efficiency and motivation to patrol their areas fully and conscientiously. Regular donations to the ranger clinic helped to build up a sustainable stock of drugs. From 2006–2009, GPP provided gear and rations as an incentive to guard remote forests; this was so successful that the scheme was adopted by the National Park Service in 2010. Further funds were raised to erect two permanent "rotary camp" shelters for rangers, in 2010 at Mayo Kam and in 2014 at Yakuba.

As well as aiding park management and conservation efforts, hybridising support for research and law enforcement has also benefited those living in this remote region, as GPP has led the development of important infrastructural improvements. Of particular importance is the fact that, in 2005, the project established an extensive radio communication system across the park and its buffer zone. This was facilitated through cooperation with Julius-Berger-Nigeria (JBN), who sponsored the installation and maintenance of the network covering about 10,000 km^2 across the park and its buffer zones. In a project spanning several years, a repeater station was erected on a mountaintop in the park's heart and hand-held radios distributed (2005), landrover-radios were acquired (2008), and ranger stations fitted with solar-powered stationary radios (2009). This not only enabled researchers to coordinate across vast tracts of forest but, crucially, enhanced the capabilities of rangers to protect this unique biotope. Moreover, in a region where messages normally travel at walking speed and mobile phones don't work, reliable radio coverage has allowed notice of medical emergencies to be provided and transportation arranged from the edge of the forest to the nearest health facilities; locals and rangers can cite examples of victims of snake bites and women in childbirth receiving urgent medical care due to radio communication being in place.

Since its inception, GPP has encouraged knowledge transfer leading to the recruitment and training of a new generation of park management and conservation experts in Nigeria. Since 2008, 30 African students have received bursaries sponsored by industry and donations and administered through GPP. Ten later entered conservation or park management careers, while 13 proceeded to higher education.

GPP likewise initiated German-Nigerian cooperation in the field of solar engineering. Students of the Oskar-von-Miller Schule, an engineering polytechnic in Kassel, Germany, designed a sustainable "power-island" ensuring a clean, uninterrupted electricity supply to the research station. Supported by JBN and German industries, the facility was installed in 2005, and was still working as of March 2018. In the course of this initiative, 11 German students have received accreditation as solar engineers and several Nigerian park personnel were trained in renewable energy techniques.

GPP also contributed to wider conservation goals in West Africa through the development of the Regional Action Plan for the Conservation of the Nigeria-Cameroon Chimpanzee (Morgan *et al.* 2011).

Finally, another GPP-related activity should be mentioned, as conceived and managed by me: artist residencies at the GPP field station. In 2010, GPP entrusted me and my partner, the curator Luiza Teixeira de Freitas, to initiate a dialogue between science and arts, by inviting artists to spend some time in the remote forests of the park and to interact with researchers. The first residency by Mexican artist Damián Ortega led to the exhibition "Apestraction" at the Freud Museum in London in 2013 (UCL Anthropology 2013). Argentinean artist Amalia Pica visited Gashaka in 2014, together with Mexican film maker Rafael Ortega. The result of this journey was Amalia Pica's exhibition "At Arm's Length", shown in 2017 at the NC-arte gallery in Bogotá, Columbia (UCL Anthropology 2017, Pica 2018). Both exhibitions featured natural objects the artists had collected in the park, in particular intricate sculptures worked from ant- and honey-harvesting tools abandoned by the chimpanzees. These shows generated considerable media interest. The programme continues and more exhibitions are likely to follow.

Thus, while there have been drawbacks, it is nevertheless true that since the start of GPP, wildlife in the central regions of the park has remained stable, particularly compared to other West African sites where, for example, the decline in chimpanzees has been as high as 90% in 15 years (Campbell *et al.* 2008). Whilst this cannot be linked exclusively to actions of GPP, a recent survey of 109 areas hosting great apes showed that GPP model – engaging local communities and supporting under-resourced law enforcement while maintaining a permanent research presence – is the most effective conservation method (Tranquilli *et al.* 2012).

With such developments, GGNP represents yet another primate study site where researchers sat out to investigate scientific questions, only to realize that the very animals and plants they were aiming to observe are in danger of disappearing. The GPP project thus encountered the same fate like the famous pioneering primatological field studies initiated by the "trimates" Jane Goodall, Dian Fossey, and Biruté Galdikas in Tanzania, Rwanda and Indonesia – which led their dedicated researchers to become dedicated conservationists, redirecting much time and effort from scientific investigation to nature protection efforts (Fossey 1983, Goodall 1986, Galdikas 1995; for GGNP, see the account of GGP's founding director, Sommer 2008).

In sum, research conducted in the Gashaka-Kwano area of Gashaka Gumti National Park (GGNP) in northeastern Nigeria has combined various sets of long-term data, a crucial foundation and addition to the research output of the *Gashaka Primate Project* (GPP) with runs into hundreds of publications already, including close to 70 peer-reviewed articles (see *Appendix*). All these efforts have helped to arrive at a more complete picture of the study site's habitat ecology and its influence on ungulate and primate patterns of reproduction, activity and sociality.

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APPENDIX I

PUBLICATIONS.

GASHAKA PRIMATE PROJECT (1999–2018)

Reference date: 01Apr2018

A total of 217 publications are listed chronologically within the following categories:

2 books,

65 research articles in journals and edited volumes,

22 unpublished reports,

15 PhD theses (completed),

4 PhD theses (expecting completion),

39 master dissertations and Diplomarbeiten,

4 undergraduate dissertations,

45 abstracts,

4 contemporary arts pieces,

13 popular writings,

4 documentaries.

Books

Sommer, Volker (2008). *Schimpansenland. Wildes Leben in Afrika*. Munich: C. H. Beck. 251 pp, 8 plates. ["Chimpanzeeland. Wild life in Africa"]

Sommer, Volker & Caroline Ross (eds.) (2011). *Primates of Gashaka. Socioecology and Conservation in Nigeria's Biodiversity Hotspot*. (Developments in Primatology: Progress and Prospects 35) Springer: New York. 531 pp

Research Articles in Journals & Edited Volumes

Sommer, Volker; Jeremiah Adanu, Isabelle Faucher & Andrew Fowler (2004). The Nigerian chimpanzee (Pan troglodytes vellerosus) at Gashaka: Two years of habituation efforts. *Folia Primatologica* 75: 295–316

Arnold, Kate & Klaus Zuberbühler (2006) The alarm calling system of adult male putty-nosed monkeys, *Cercopithecus nictitans martini*. *Animal Behaviour* 72: 643–653

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Fowler, Andrew & Volker Sommer (2007). Subsistence technology in Nigerian chimpanzees. *International Journal of Primatology* 28: 997–1023

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Higham, James P.; Michael Heistermann, Caroline Ross, Stuart Semple & Ann MacLarnon (2008). The timing of ovulation with respect to sexual swelling detumescence in wild olive baboons. *Primates* 49: 295–299

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Higham, James P. & David M. Bennett (2008). Perspectives on wildlife, and wildlife consumption, in Eastern Nigeria. *Gorilla Journal* 36: 11–13

Wilkinson, Roger (2008). Some recent records of birds from Gashaka Gumti National Park and Ngel Nyaki, Nigeria, and the Gotel Mountains, Cameroon. *Malimbus* 30: 156–164

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APPENDIX II

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