

Antelope Predation by Nigerian Forest Baboons: Ecological and Behavioural Correlates

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Abstract

Baboons are well studied in savannah grasslands, whereas little is known about their ecology and behaviour in less open habitats, particularly forest, into which baboons penetrate at the edges of their distribution. We investigated predation on mammals by olive baboons (*Papio anubis*) at a geographical and climatic outlier, Gashaka Gumti National Park in Nigeria, which represents the wettest and most forested baboon study site so far. Here, despite an abundance of wildlife, meat eating was found to be very rare and selective. Over a 16-year period, baboons killed 7 bushbuck (*Tragelaphus scriptus*) and 3 red-flanked duiker (*Cephalophus rufilatus*), probably all infants. Taking observation time into account, this translates into a frequency of one predation per troop every 3.3 months – far lower than at other sites. Some features of meat eating resemble those elsewhere. For example, predation is opportunistic, adult males monopolise most prey, a targeted killing bite is lacking, and while bystanders obtain scraps of meat, begging or active sharing is absent. Moreover, carcass owners employ evasive tactics, as meat is often competed over. Satiated owners may tolerate others grabbing the carcass, as in the context of male-female and mother-offspring interaction. Various other features are unusual. For example, this is only the second study site with predation records for bushbuck and the only 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. Baboons at this site may therefore be restricted to predation on still-lying "parked" infants that are opportunistically encountered. Our data support the general prediction of the socioecological model that environments shape behavioural patterns, while acknowledging intra-specific or intra-generic plasticity.

Introduction

Socioecology, the study of how an individual's interaction with its environment shapes the society it lives in (Crook & Gartlan, 1966), is central to primatology. The socioecological model assumes that similar ecological conditions will produce similar patterns in terms of social systems. This approach generated a wealth of predictions and concomitant categorizations of species or genera (Dunbar 1988). However, as more field studies were conducted, variations in social systems came to light, both within species and within

populations, and it became evident that primates do not always fit easily into distinct categories. This triggered successive modifications and critiques of the classic model, either through refining measurements of ecological variables or by considering how phylogeny constrains phenotypic variation [Koenig & Borries, 2009; Clutton-Brock & Janson, 2012].

Documenting the flexibility and variation of behaviour of the same species across populations and across different members of the same genus can make an important contribution towards disentangling the relative importance of phylogeny versus ecology. We add to this debate by providing data on meat eating [Fichtel, 2012] in baboons. Given the close evolutionary relationship of different baboon taxa, we predict that the environment – and not phylogeny – is the most likely cause for possible variations of predatory behaviour [Chapman & Rothman, 2009].

Baboons (genus *Papio*) are Old World Monkeys of the family Cercopithecidae (cheek pouched monkeys) that are widely distributed across Africa and into the Arabian peninsula. Traditionally recognized and phenotypically distinct morphotypes include hamadryas or sacred (*P. hamadryas*), Guinea (*P. papio*), chacma (*P. ursinus*), yellow (*P. cynocephalus*) and olive or Anubis baboon (*P. anubis*) [Zinner et al., 2011; see also Oates, 2011; Kingdon, 2015]. Except for hamadryas and Guinea, baboons have a basic social structure of multi-male-multi-female groups based on female philopatry and male migration. A comprehensive review of baboon predatory behaviour is beyond the scope of this paper, which primarily aims to broaden the available database by providing additional and detailed empirical information. Nevertheless, we selected publications that document predatory behaviour across the 5 baboon taxa to ascertain general features of habitat ecology and prey selection. This preliminary review (table 1) reveals that baboon prey species include at least 3 primates, 10 ungulates, 4 rodents, 3 hares, 1 bat, 4 species of herpetofauna and 6 species of bird. Of 329 individually identified prey animals, 83.0 % were mammals, 4.6 % herpetofauna and 12.5 % birds. The most common prey type were ungulates (41.0 %; mostly immature antelopes, but also domestic goats and sheep), followed by hares (25.5 %), birds (12.5 %) and other primates (9.1 %). In 18 studies reviewed for reports on predation, 87.0 % of the habitats fell in the category "open", including grassland (56.5 %), farmland, desert, riverbeds, beach (17.4 %) and woodland (13.0 %). Only 13.0 % of prey habitat was "closed", i.e., forests, from where reported predation

events accounted for only 7.4 % of the total.

This bias is not surprising, given that baboons are well studied in open habitats, particularly savannah grassland, where behaviour is relatively easy to observe. However, little is known about baboon ecology and behaviour in less open environments, such as forests, into which baboons penetrate to various extents at the edges of their distribution [Higham et al., 2009]. Here, we present the first data on mammal predation by wild olive baboons inhabiting a relatively closed environment. The study site in Northeastern Nigeria is an outlier in terms of habitat and climate. Our research is based on long-term observation of two well-habituated troops [Sommer and Ross, 2011]. For our analyses, we compare ecological features such as climate, plant cover and potential prey species across the geographical and taxonomical range of baboons against our study population living in a marginal environment at the edge of the genus' geographical distribution. As such, our data should be of interest for understanding if and how environmental factors influence variation in baboon predatory behaviour.

Methods

Study Area: Gashaka Gumti National Park / Nigeria

Our data on carnivorous behaviour of olive baboons were collected in Nigeria in the mountainous Gashaka sector of Gashaka Gumti National Park (GGNP, 06°55' – 08°13' N and 011°13' – 012°11' E; fig. 1). GGNP represents the northern edge of the Cameroonian Highlands and the Gulf of Guinea forests [Sommer & Ross, 2011a]. The park encompasses 6,731 km², and includes various village enclaves, mainly inhabited by settled Fulani cattle herders.

In GGNP, pronounced wet and dry seasons correspond with fluctuations in temperature and humidity [Sommer & Ross, 2011]. In the Gashaka study area, between 2000–2014, mean minimum temperature was 20.9 °C, mean maximum 32.5 °C, and annual mean rainfall 1,945 mm (range 1,681–2,337 mm). As for seasonality, five months with very little or no rainfall are

followed by heavy downpours from mid-Apr to mid-Nov that constitute 97.2 % of all precipitation.

The vegetation cover of the Gashaka sector of the park is a mosaic of Southern Guinea woodland-savannah, riverine and lowland rain forest, montane forest as well as grassland [Adanu et al., 2011]. The habitat of GGNP with its extensive forests is unusual for baboons, and also represents the wettest of all baboon study sites to date [Higham et al., 2009]. Disease, perhaps brought about by high rainfall [Higham et al., 2009], as well as inter-specific competition might be likely reasons why baboons are often excluded from closed forests [Kingdon, 2015]. The GGNP population lives close to the southern edge of the species' western biogeographical distribution [Zinner et al., 2011]. Just a short distance to the south, baboons disappear, replaced by large forest-dwelling monkeys, in particular drills (*Mandrillus leucophaeus*).

Study Troops: Kwano and Gamgam

Since the year 2000, we collected data on two baboon troops in GGNP (see, e.g., [Higham et al., 2009; Warren et al., 2011; Ross et al., 2011]), *Gamgam* troop (in previous publications sometimes referred to as "Gashaka troop" or CR [crop-raiding] troop) and *Kwano* troop (previously NR [non-raiding] troop). The troops live about 10 km apart, with Gamgam's range around 1 km outside the national park boundary, and Kwano's range inside the park (fig. 2).

Troop home ranges differ somewhat in altitude (Kwano 583 m, Gamgam 320 m), mean annual rainfall (Kwano 1,977 mm, Gamgam 1,913 mm; data for 2000–2014) and size (Kwano 1.9–2.6 km², Gamgam 1.8–2.5 km²; data for 2009–2010 [Alberts, 2012] and 2012 [GJ, in prep.]). Troop sizes varied, depending on birth, death, immigration and emigration. For example, between 2000–2008, they averaged 28.4 animals for Kwano (range 26–35) and 19.3 animals for Gamgam (range 14–23). The across-troop average was 24.3 animals, including an average of 6.2 adult females [Warren et al., 2011].

All troop members were known individually. For the purpose of this report, age-sex classes are defined as follows [Warren et al., 2011]: IM = infant male (birth – 2 yrs), IF = infant

female (birth – 2 yrs), JM = juvenile male (>2 – <6 yrs), JF = juvenile female (>2 – <4 yrs), AM = adult male (6+ yrs), AF = adult female (4+ yrs).

The home ranges of both troops encompass various proportions of forest and woodland. Data from an 8-km random line transect show a greater density of forest trees (mean floor-area / tree 31 m², range 6–100 m², SD 20, n = 801), compared to trees in woodland (mean floor-area / tree 48 m², range 17–100 m², SD 28, n = 181). However, visibility is not necessarily better in woodland, because each year, much of its grass cover is deliberately burned for about 3 months (Dec-Feb). This encourages the dominance of a single grass species, the African dropseed (*Sporobolus africanus*), which often grows 2 m high and densely blankets the habitat from May–Nov.

The proportion of forest to woodland is 72 % to 28 % for the Kwano range versus 18 % to 82 % for Gamgam. In addition, Gamgam troop regularly supplements its diet with maize and a variety of other crops, including subterranean items, taken from fields along the banks of the Gamgam river (which constitute about 15 % of its home range).

Such differences notwithstanding, study troop baboons spend similar percentages of feeding time on principal food types (K = Kwano, G = Gamgam): leaves (K 6 %, G 4 %), flowers (K 5 %, G 5 %), fruit and seeds (K 63 %, G 54 %), subterranean items (K 1 %, G 6 %), invertebrates (K 8 %, G 14 %) [Ross et al., 2011]. Members of all age-sex classes consume invertebrates such as *Lepidoptera* caterpillars and cocoons (57 %), aquatic fauna including crabs (20 %), *Scarabaeidae* beetle larvae (13 %) as well as other insects including ants and termites (9 %) [Ross et al., 2011].

Observations of both baboon troops were conducted for about 10–20 days / month, each observation period typically lasting at least 6 h, from either 06:00–12:00 or 12:00–18:00. Data collection followed a routine executed by trained field assistants who may or may not have been accompanied by students, researchers or volunteers. For example, between 2004–2011, observation time on troop Kwano amounted to 4,147 h and for troop Gamgam to 3,596 h. The combined total of 7,743 h translates into 968 h / yr or 2.7 h / day. The comprehensive observation schedule renders it likely that we obtained representative records even about relatively rare events such as predation. Nevertheless, the detail of recorded information varied from case to case.

Background Data: Potential Mammalian Prey Species

Baboon troops that range near villages in and around Nigeria's GGNP often come into contact with *domestic animals*. Project field assistants Hammaunde Guruza, Maigari Ahmadu and Halidu Iiyasu, who grew up in Gashaka in farming families, report that monkeys will occasionally kill and eat chickens (*Gallus gallus domesticus*) as well as goats (*Capra hircus*) and sheep (*Ovis aries*) (mostly immature individuals, but also some adults; similarly reported by [Akosim et al., 2010] for baboons in Nigeria's nearby Adamawa state). The typical hunting strategy involves sitting still until the potential prey is close enough so that it can be leapt at and caught, as well as chasing prey that aims to escape. Baboons in and near GGNP have also killed dogs (*Canis familiaris*) that confronted them, and they have bitten human children and women. There are no reports about attacks on cows (*Bos taurus*) or horses (*Equus caballus*). In one instance, a troop in open grassland was seen running after and catching a scrub hare.

Thus, given that GGNP baboons can kill and eat relatively large animals, we expect the study troop monkeys to have similar abilities. Table 2 lists species of 5 orders of mammals that occur in their home ranges. Baboons elsewhere in Africa prey upon members of these orders (cf. table 1), albeit not necessarily the same species as those found at the Nigerian site. Still, it seems reasonable to expect that study troop baboons are motivated to kill and consume individuals of some of these species.

For these study area mammals, the tabulation also lists body dimensions and the number of animals typically seen together. These factors likely influence the probability that baboons encounter and overpower such potential prey animals. Data on mammal group sizes were collected by varied means. While not standardised across taxa, these figures nevertheless broadly indicate the degree of sociality of potential prey species. (a) Foot surveys of large mammals in the wider Kwano study area by field assistants and researchers totalling 14,493 h over a 4-yr period (2005–2008). This translates into 3,623 h / year or 9.9 h / day. For these surveys, typically a single observer (and sometimes teams of 2–3 individuals) went on predetermined routes that systematically covered quadrants of a 30 km² area. Observers followed a

rota of walking and pausing, while recording sightings of pigs, antelopes and primates. Surveys encompassed all hours of the daytime and all months of the year. (b) These survey data are supplemented for some taxa (giant forest hog, bushbuck, yellow-backed duiker) through records from a still-camera trap placed in front of a mineral lick within the Kwano baboon troop range over a 5-month period (2011, 2013). Group sizes calculated from camera trap images and foot surveys were found to be very similar. (c) Counts for some rarely seen animals (blue duiker, squirrel) are based on opportunistic records from 20 video-camera traps placed across the wider Kwano habitat for 3 years (2012–2014). (d) Data for putty-nosed monkeys, mona monkeys and colobus monkeys reflect systematic group counts in the wider Kwano study area along a standardised 9.5 km route, evenly spread across the daytime, executed by Jeremiah Adanu over an 8-month period (May–Dec 2000). (e) Counts for chimpanzees and the study baboons themselves are based on published long-term data.

Records during successive days might capture the same individual animals or groups. However, the counts still provide a fair indication about probabilities with which study baboons, during their daily travels, encounter certain types and numbers of animals. These can be compared against actual rates with which baboons capture and consume prey. This, in turn, will inform conclusions about opportunities and constraints that study troop baboons face with respect to predatory activities.

Apart from mammals, baboons elsewhere in Africa also eat non-mammalian vertebrates (cf. table 1). We will therefore also report instances in which study troop baboons preyed on herpetofauna, reptiles or birds.

Manuscript Preparation

Baboon research at GGNP is directed by senior author Caroline Ross. Gonçalo Jesus collated the data for mammalian group counts and baboon observation frequencies. The report was compiled by lead author Volker Sommer who also manages the site's long-term data. All other authors observed and recorded one or more predation event.

RESULTS

Predation on Non-Mammalian Vertebrates

Adult, subadult and juvenile study troop baboons of both sexes occasionally catch and eat small lizards such as the common agama (*Agama agama*; individual monkeys of Kwano troop caught lizards on, e.g., the following days: JM Rabi 04Mar07, 01May07; AF Ymke 08Mar07; AF DrKate 09Apr07; AM Baki 01 Mar07, 03Apr11; SM Sama 07Apr11). On two occasions, study troop baboons have been seen to kill and eat Guinea fowl and they were seen once to consume eggs of Guinea fowl and once an unrecognized pigeon-like bird. There are no observations of baboons killing snakes, frogs or fish, despite an abundance of such animals in their home ranges.

Predation on Mammals

Baboons of troops Kwano and Gamgam regularly come into visual and close spatial contact with other mammals such as primates and ungulates (fig. 3a). However, they hardly ever display visibly heightened interest (fig. 3b). Study troop baboons have never been observed to pursue, i.e., actively "hunt", any sympatric large mammal, although on one occasion, Kwano troop baboons were seen chasing after a civet (*Civettictis civetta*) for unknown reasons (pers. comm. by field assistant Halidu Iliyasu).

Still, over a 16-year period, study baboons are known to have obtained and eaten 10 antelopes, at least 9 of them infants. A summary of the cases described below as well as details on date, observer and troop composition are provided in table 3.

Case 1 (red-flanked duiker). – A field assistant hears antelope distress calls while at the riverbank. Upon walking towards the sound, he encounters an AM baboon with a dead duiker infant. The AM monopolises the carcass and threatens other approaching baboons. *Case 2 (bushbuck).* – AM Dogo is seen eating infant bushbuck, while other baboons surround him.

Case 3 (red-flanked duiker). – 2 AM and AF Bera drag parts of a red-flanked duiker carcass (infant?) across ground, i.e., a leg and hindquarter, while intermittently consuming the body parts.

Case 4 (bushbuck). – Ca. 10:00: AM Sanda catches screaming infant bushbuck. He holds it to ground and bites into top of the skull, killing it. AM Sanda then sits in undergrowth, eats front half of carcass. No disturbance by other baboons. AF Lami (with infant) sits within arm's reach, away, AF Sadiya and AF Ymke within 5 m. AF Sadiya comes close but AF Lami chases her off. – AM Sanda strips off meat from joints of one leg while holding it in both hands, with carcass between his feet. Occasionally, smaller bones crack between his teeth. – JM Jolly and JM Bonny watch from within 5 m, while JF Tala sits on a branch just above the ground, manipulating a small piece of meat. JF Tala drops it, picks it up, rubs it between hands and along a branch, as if to clean it. She eats and continues picking at the meat as if playing. – AF Sadiya, having not had access to the meat, licks blood from leaves on ground. – 11:50: AF Lami (with infant) grooms AM Sanda for about 5 min. She then takes bulk of carcass and consumes meat. AM Sanda follows but does not attempt to retrieve it. He stays within 5 m of AF Lami while she drags carcass around when approached by others. For the next half hour, she intermittently strips flesh from small bones and eats. No other individuals get access to carcass. No aggression over meat witnessed. – 12:20: AF Lami sits alone, with full cheek pouches, eating bones.

Case 5 (bushbuck). – Bushbuck distress calls heard. AM baboon is seen with infant bushbuck. The fawn's mother remains in vicinity, tries to approach, but other baboons chase her until she runs away.

Case 6 (bushbuck). – Ca. 11:15: Observers go towards where they hear screams of infant bushbuck. They see AF Mamakane holding down an infant bushbuck. She bites into the top of its head, then eats for the next half hour. – 11:45: AF Mamakane has dragged carcass into a patch of gallery forest, and onto a vine over a dried-up riverbed. JM Leo (AF Mamakane's son) sits underneath, looking up and around for scraps of meat. 11:50: AF Kane and IF Diana (AF Mamakane's daughter and granddaughter) arrive to sit directly underneath the vine, occasionally touching the legs of the carcass (fig. 4a). SM Augustine, who has also arrived, stays at about 2 m distance. – 11:51: AF Mamakane moves into the woodland with carcass in

her mouth. Over the next 2 h, she opens up the prey's belly (fig. 4b) to consume its contents and the antelope's neck, while periodically changing location. AF Kane and IF Diana remain close, as do JM Leo and JM Augustine, who at times eat left-behind scraps. – 14:04: The ribs of the bushbuck are now visible. AF Mamakane continues to feed on the largely depleted contents of the belly before abandoning the carcass. JM Leo now carries it a small distance to consume remains of the belly and spine, while appearing vigilant and nervous. He carries the carcass off in his mouth when AM Darwin approaches, then leaves it at the base of a tree, before climbing up. 14:23: AM Darwin feeds on the remains and occasionally moves with the carcass. More juveniles approach, as do AF Kane and IF Diana, who are chased away by AM Darwin. 14:28: He leaves with the depleted carcass. Observers do not follow.

Case 7 (bushbuck). – Earlier in the day, bushbuck calls are heard in area where baboons are later found by observers. When troop is encountered, AM Kasa is seen eating infant bushbuck. AF Lami grooms AM Kasa, who moves off with carcass, but leaves some meat for AF Lami. Later, AF Bera and JM Jamilu also obtain some meat. – A juvenile male carries around leftover bits of the carcass for days.

Case 8 (red-flanked duiker). – 09:00: Baboon troop scattered in open woodland. AM Fedi runs towards a depression (ca. 0.7 m deep, 2 m long, 1 m wide), from where an adult duiker female flees. – Baboons whao-bark and scream, while one adult pursues the fleeing antelope. Duiker infant distress calls heard. – 09:03: At the depression's edge, AM Fedi is whao-barking while restraining a screaming duiker infant. – 09:12: AM Fedi grabs duiker infant's hind legs with both hands while its head points away from the baboon's chest; AM Fedi scans surroundings, probably watching out for approaching troop members. AM Darwin dashes by. – 09:18: AM Fedi bites into infant's back (fig. 5a), swerves his own body and that of prey 360 degrees, before biting the back again; infant bleats continuously. – 09:29: Several baboons whao-bark; the adult duiker female (presumably the infant's mother) runs zigzag through the grass. – 09:32: Duiker female runs briefly towards captured infant, but changes direction when 3 baboons give chase. Female escapes into nearby forest edge. – 09:41: AM Fedi bites into infant's left thigh, runs towards forest edge, while screaming infant dangles from his muzzle. – 10:00: On ground, AM Fedi crouches over screaming duiker, bites forcefully into infant's rump; he scans surroundings, lip-smacks towards an adult baboon passing by; AM

Fedi restrains duiker's hindlegs with both hands, before lifting the antelope, grasping around its neck with both hands. – 10:10: AM Fedi positions infant head near muzzle, while duiker flings front legs. He bites into top of infant's skull, accessing and ingesting brain matter (fig. 5b); duiker screams terminate, body slumps and becomes lifeless; AM Fedi chews, some white brain matter drips from his mouth. Over the next hour, AM Fedi bites another 4 times into the top of duiker's head (10:18, 10:39, 10:51, 11:01), while accessing and ingesting more brain matter, intermittently licking the head area and fingers of his own left hand, chewing and scanning surroundings. 11:28: Another adult baboon passes by, without trying to intervene. Soon after, other baboons approach. – 12:30 onwards: AM Fedi climbs tree, holding prey, settles about 2 m above ground, on vertical branch, ca. 2 m away from trunk. Sitting upright, holding carcass at its neck, with rump dangling down, AM Fedi nibbles at duiker's head, intermittently chewing. Other baboons climb tree, try to approach AM Fedi, with unknown outcome. On ground, AF Straighttail and AF Budurwa feed on scraps. – Observers leave at this point.

Case 9 (bushbuck). – Observers hear screams of bushbuck, probably including adult. Upon arrival at scene, AM Dali is seen on ground, holding infant bushbuck at neck and biting into top of head. AM Dali consumes prey for some time. Other troop members obtaining pieces of meat are AF Ladi, JM Daji, JM Nawa. Little remains of carcass when observers leave.

Case 10 (bushbuck). – 06:30: Patch of woodland on forest edge. Most baboons are still in sleeping trees. Screams of infant bushbuck are heard; several adult baboons run towards the noise. There is no sign of the mother. – 06:37: AM Erni emerges with carcass, runs up a tree where he begins to eat (fig. 6a). Another adult sits near him in the canopy but does not approach too closely. AM Erni grunts loudly, evidently a warning to others to keep their distance. AM Erni drops carcass; other adults approach but he retrieves it and chases them off. AM Dali picks up meat scrap tastes it but does not eat it. – 06:39: AM Erni moves off repeatedly with carcass whenever approached by baboons or observers. – 06:52: AM Erni eats in undergrowth, first head, then flank, then slices open the belly (fig. 6b). AF Ymke with IF Gaetane sits within arm's reach but does not attempt to touch the meat. Infant sniffs the carcass but is ignored by AM Erni. AM Garrido and AM Dali approach aggressively. Both grunt, as does AM Erni. AM Erni runs off; AM Garrido and AM Dali chase him through

undergrowth, barking loudly. AM Garrido obtains the carcass, runs up a tree and eats the remainders. – 07:55: Other adults and juveniles including at least 2 AF and 2 JM sit below him, on branches and ground, picking up scraps (fig. 6c). The majority of the troop stay close throughout and watch this activity intently. AM Garrido repeatedly changes position in the tree and grunts whenever anyone else approaches. AM Dali circles on the ground, staring and grunting. He displaces juvenile males sitting under AM Garrido and the meat. He gets scraps and picks at blood-stained leaves. – 08:40: AM Garrido leaves tree; at this point the carcass is mostly skin and fur. He walks into the undergrowth (fig. 6d). A JM runs up, apparently trying to steal the meat, resulting in aggressive grunts from AM Garrido and loud screams by the JM. Others run towards the noise. The whole troop moves off into the forest. When located again by observers, the carcass is gone.

Seasonal Frequency and Habitat Type of Antelope Predation

The predation events represent a rate of one killing of antelope per every 1,291 h of observation. Given an average of 12.5 daylight hours, this translates into a rate of one killing every 103 full days. As for yearly quarters, kill proportions were as follows: Jan–Mar (dry season) 16 %; Apr–Jun (early rainy season) 60 %; Jul–Sep (rainy season) 0 %; Oct–Dec (late rainy season) 25 %.

Compared to the overall proportions of habitat type, killings in closed forest are overrepresented by 30 %, while those in open woodland are proportionally underrepresented by 30 %. This contrasts with the likelihood that observers encountered (adult) prey antelopes in these habitats during the 2005–2008 foot surveys (see Methods), as sightings of bushbuck were underrepresented in forests by 24 % and those of red-flanked duiker by 18 %.

Discussion

In the following, we compare the site-specific ecological and behavioural correlates of meat eating at GGNP (cf. table 2, table 3) with other baboon study sites (cf. table 1), to discern if

and why predation pattern might vary. Our analyses support the assumption that environmental factors are a main influence on predatory behaviour of the two baboon study troops.

Meat Eating

With regard to non-mammalian vertebrate prey, GGNP study troop baboons occasionally killed small lizards, but hardly ever consumed birds or eggs. As for mammalian prey, despite an abundance of species, baboons killed only 7 bushbuck and 3 red-flanked duiker, probably all infants, over a 16-year study period. Taking observation time into account, this translates into a frequency of one mammal killed every 1,291 h. Despite some predation events likely going unnoticed, this is low or very low compared to other sites where a mammal is taken every 643 h [Stoltz & Saayman, 1970], 30 h [Rowell, 1966], 22 h [Harding, 1973] or even 12 h [Strum, 1975]. Mammalian meat is therefore not a regular source of nutrition for GGNP baboons, as it is obtained only about every 3.3 months.

Nevertheless, animal flesh clearly constitutes a desirable resource for GGNP baboons given that owners invariably resist sharing. Small lizards were easily monopolised by those who caught them. However, the much larger antelope carcasses were harder to control – not least, because possession ideally needed to be maintained for considerable time, given that catching and consuming until only scraps were left could take hours (case 9: 2 h, 10 min; case 4: 2 h, 20 min; case 6: >3 h, 12 min). Owners seemed to be wary about potential competition and regularly took evasive action (best observed in cases 1, 7, 8, 10). This did not always involve climbing a tree (as in cases 4, 6, 10), perhaps because carcasses are more difficult to process on a branch.

Bystanders often assumed a "vulture response" [Altmann & Altmann, 1970] by staring at the animal that ate the meat (see also [Harding, 1973; Strum, 1975]). As in other baboon populations, active begging gestures were never observed (see also [Butynski, 1982]). Still, hangers-on were able to obtain scraps of meat, in particular when an animal fed on a carcass on a branch, and parts rained down (cases 6, 10). Baboons also licked blood from vegetation (cases 4, 10). In total, other baboons than the first owner of the carcass obtained some meat

in more than half of the cases, i.e., in at least 6 instances (cases 3, 4, 6, 8, 9, 10). This included adults and juveniles of both sexes.

The bulk of the carcass passed on in at least 3 instances. In case 10, two adult males ganged up on the meat-owner, and one of the coalition partners was able to obtain the carcass. A juvenile male tried the same on his own, but was rebuffed by severe aggression (for correlations of meat intake with dominance rank, see [Hamilton & Busse, 1982]). In case 6, the carcass passed on from the original owner, an adult female, to her juvenile son (for similar non-aggressive "sharing" with offspring, see [Strum, 1975]). In case 4, the owner was groomed by an adult female, who then made off with the carcass. Interestingly, the meat-deprived male showed little effort to retrieve the prey. Grooming a meat owner might be a female strategy, as this behaviour was observed one other time (case 7); in this instance, the female groomer did not obtain the carcass, but did get some meat the owner left behind. Baboon females in other populations have likewise been observed to steal meat from males after relaxing them through grooming [Strum, 1984; Byrne & Whiten, 1990]. Whether this is re-paid somehow, perhaps via sexual favours, is unknown, but conceivable (see, e.g., [Smuts, 1985] for baboons; for mechanisms and functions of primate food sharing in general, see [Jaeggi & Gurven, 2013]).

Prey Acquisition

We have no indication of active hunting where prey is run down, let alone in the coordinated relay-chasing fashion previously observed in East African baboons [Strum, 1975]. This may explain why no adult antelopes are killed. Still, such a lack is puzzling because baboons regularly come near to full-grown ungulates (cf. fig. 3c). However, proximity might not be as close as with domestic sheep and goats, which baboons kill by lunging at when they pass by. Moreover, wild ungulates might be aware that baboons are predators and therefore maintain a critical distance.

The type of prey acquisition could be reconstructed for roughly half of the 329 prey animals listed in table 1. Thus, independent from baboon species, about 40 % of prey animals were spotted and then chased, while 60 % were grabbed after the monkeys encountered them by chance, e.g., when they were flushed out from grass. GGNP baboons always encountered

their mammalian prey opportunistically, typically while foraging. Bushbuck infants, at least in Kenya, spend time in concealment away from their mothers during the first few weeks of life [Allsopp, 1978; see also Waser, 1975]. Infant-parking while mothers forage is also likely a regular occurrence at GGNP, at least for red-flanked duiker, because observers never encountered mothers with babies (cf. table 2; neonates of blue and yellow-backed duiker were likewise never seen). Instead, 90.2 % of all sightings were of single adults and the rest pairs (cf. table 2). Moreover, duiker use freezing as a predator avoidance strategy [Croes et al., 2007; Kingdon, 2015]. Thus, whether young are "parked" or mother and infant freeze: kills typically happen when baboons are "quite literally tripping over their prey" [Harding, 1973: 588] (see also [Goodall, 1986], for chimpanzees stumbling over bushbuck fawns). This antelope-typical pattern of infant rearing might explain why ungulates represent such a large segment of prey animals for baboons across Africa (41.0 %; see table 1).

In fact, immature animals constitute the vast majority of prey animals for all baboon species. Age can be discerned for 112 (34.0 %) of 329 prey animals listed in table 1. Of these, 89.2 % were non-adults ("fledgling", "neonate", "infant", "juvenile", "subadult"). The proportion of immature individuals within different clades was as follows: primates, 100 % (n = 18 prey animals); ungulates, 100 % (n = 75; a further 9 animals were of various ages); hares, 67 % (n = 3; a further 12 prey animals were of various ages); rodents 0 % (n = 11).

Although adult duiker and bushbuck are seen throughout the year in the GGNP study area, predation is highly seasonal, occurring mainly during the early rainy season (Apr–Jun) with a smaller peak during the late rainy season (Oct–Dec) (cf. table 3). As infants constituted 90–100% of the prey animals, this is probably due to a lambing peak. In East and Southeastern Africa, free-ranging or wild bushbuck and common duiker breed throughout the year. Still, duiker have a lambing peak in the dry season (Mar) and another one in Oct–Nov [Dasmann & Mossman, 1962; Bowman & Plowman, 2002], while bushbuck lambing peaks twice, in Feb and Sep [Ables & Ables, 1971]. However, in Uganda, bushbuck lambing peaks during the onset of the rainy season [Apio et al., 2009]. Such birth seasonality coincides well with our own data on predation.

During the inferred wet-season lambing peak at GGNP, woodlands are blanketed by tall grass [Sommer & Ross, 2011], which provides 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. Although we do not know if lambs are predominantly parked in forest or woodland, this supports an earlier hypothesis [Hausfater, 1976] that declining cover leads to increased predation rates by baboons. Nevertheless, we also cannot exclude that baboons obtain their prey predominantly in forest simply because both troops travel preferentially in gallery forest [Alberts, 2012].

However, like other studies (e.g. [Rhine et al., 1986]), we did not find support for the hypothesis that a reduced availability of green vegetation and insects during the dry season causes increased meat eating [Hausfater, 1976] – given that dry season predation was relatively rare at GGNP. Instead, it seems more likely that lambing peaks reflect synchronization of parturition with the time when suitable food is available to the lactating mother or her soon to-be-weaned calf. Duiker are generally frugivorous, with fruit making up to 78% of the diet [Wenninger & Shipley, 2000], while bushbuck prefer to browse on shrubs and herbs [Apio et al., 2009]. Thus, it is not surprising that antelope predation at GGNP peaks with the onset of the rainy season when fresh herbs and shoots are more abundant and when fruit production of study area trees and associated vines is highest [Sommer et al., 2012].

The crypsis of parked duiker and bushbuck fawns gives way to frantic bleating and screams once they are caught (cases 1, 4, 5, 7, 9). However, mothers are unable to aid caught offspring as they were chased by other baboons when they ran towards their infants (cases 5, 8). Nevertheless, the baboons are clearly struggling to retain caught antelopes, evidently lacking a strategy to quickly immobilise their catch. Instead, prey owners endeavour to restrain prey by pressing it to the ground or holding it by its hind legs or neck (cases 4, 6, 9). Baboons at other sites do not appear to make any systematic attempt to kill their prey before eating it either [Harding, 1973]. Whenever an actual killing was witnessed (cases 4, 6, 8, 9), baboons bit into the top of the infant's skull. This happened a while after the prey was caught, perhaps because the owner first tried to find a location relatively undisturbed by troop mates. Thus, skull-bites should not be interpreted as a targeted killing bite, but as an effort to obtain the most desirable body part, i.e., the brain (similar to chimpanzee meat eating; e.g., [Goodall, 1986]). This conflicts with reports for baboons at Gilgil / Kenya, where antelope brain was

generally eaten last [Harding, 1973], while the skull was not at all accessed at Amboseli / Kenya [Hausfater, 1976]. Still, the question remains why an immobilizing bite is not administered before the prey is carried off to a convenient spot.

As for potential sex-differences, adult females are the main catchers and killers of mammals in bonobos [Hohmann & Fruth, 2008], while adult males take up this role in chimpanzees (e.g., [Stanford, 1998]) and human hunter-gatherers (e.g., [Power et al., 2013]). As for baboons, the catcher's age-sex class was specified for 197 (59.8 %) of the 329 prey animals listed in table 1. Overall, adult males caught 79.2 % of all prey, adult females 16.8 % and younger animals 4.1 %. Noticeable differences exist with respect to prey taxa (n = number of prey animals for which age-sex class of catcher is known; % AM resp. AF = percentage caught by adult males resp. adult females): primates, n = 28, AM 100.0 %, AF 0 %; ungulates, n = 81, AM 95.1 %, AF 4.9 %; rodents, n = 3, AM 33.3 %, AF 66.6 %; hares, n = 56, AM 67.9 %, AF 30.4 %; herpetofauna, n = 5, AM = 60.0 %, AF 40.0 %; birds, n = 22, AM 40.9 %, AF 27.3 %. Thus, adult females hardly ever catch larger prey such as primates and ungulates. This is true for all species of baboon.

While largely circumstantial, it seems as if adult males play also a more active role in antelope predation at GGNP, given that they caught them in the two actually witnessed cases. When observers arrived later, an adult female owned the carcass in a single case, compared to 6 cases when an adult male owned it. However, we cannot exclude the possibility that males had taken fresh prey from females as these should come across cryptic prey with greater probability, given that study troops had an average of 4.3 adult males compared to 6.2 adult females [Warren et al., 2011]. The actual killing was executed by adult males in 4 of the 5 cases where this was witnessed and by an adult female in the remaining case. Subsequently, adult males consumed meat for much longer than other age-sex classes.

It seems likely that these sex differences are due to the much larger body size and fighting power of adult male baboons and perhaps that they are unencumbered by infant-care [Rhine et al. 1986]. Hausfater [1976] had hypothesized that baboon females acquire animal nutrients primarily through feeding on invertebrates, while males do so by preying on vertebrates. This suggestion is not supported by data for GGNP baboons, mainly because of the rarity of

vertebrate predation, but also a lack of apparent sex-differences with respect to invertebrate feeding [Ross et al. 2011].

Prey Species

Predatory behaviour of the Nigerian study troop baboons is evidently very specific, as only two of the many sympatric large mammal species were eaten. Various factors are likely to affect prey selection at this site.

Apart from GGNP, bushbuck consumption by baboons is only reported for Gombe / Tanzania, where it is likewise restricted to fawns ([Goodall, 1986]; cf. table 1). The Gombe habitat, like GGNP, is largely a woodland-forest mosaic, albeit noticeably drier. There are no duiker at Gombe, and there is no report on baboons consuming duiker at any other sites, which are almost all savannah habitats. As these small antelopes prefer forested areas, it is no surprise that reports of them being eaten by baboons are currently restricted to GGNP.

Still, the question remains why other study area mammals are not preyed upon. At least two taxa of these sympatric mammals are eaten elsewhere by baboons – hares and vervet monkeys (cf. table 1). However, hare species consumed at other places prefer completely open grassland, while lagomorphs at GGNP are scrub hares. These are heavier and also favour more cover such as scrubby grass within woodlands [Kingdon, 2015]. Such traits might make it more difficult for GGNP baboons to catch them. The vervet-like primates at GGNP are tantalus monkeys, who, albeit often terrestrial, can easily escape into the relative safety of trees, an opportunity lacking in more open habitats. The other monkeys at GGNP, i.e., colobus and guenons, might be even better protected from baboons because of their almost exclusively arboreal lifestyle.

Grouping patterns of potential prey (cf. table 2) may also influence which species at GGNP 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. Groups of red river hog average 5 animals, with a maximum of 13, while those of giant forest hog average 4 animals, with a maximum of 11 (cf. table 2). In fact, the only report of baboons eating suids comes from Gombe / Tanzania where baboons scavenged bushpig from chimpanzees ([Goodall, 1986]; cf. table 1). Infants of other antelopes may also be protected because they

travel with adults. Buffalo groups at GGNP average 6 animals, with a maximum of 12, while those of waterbuck average 3 animals, with a maximum of 8 (cf. table 2).

The group-size explanation for why baboons do not prey upon certain species cannot be invoked for the remaining two antelopes – yellow-backed duiker and blue duiker. These are seen at the most in pairs, but in 76 % resp. 40 % of counts as single individuals (cf. table 2). They are also likely to park their infants, as these were never seen by observers or on camera-traps. Blue duiker seem rare in the study area, as they were very rarely seen during foot surveys (cf. table 2). Yellow-backed duiker, on the other hand, were seen 2–3 times more commonly ($n = 129$ sightings) than bushbuck ($n = 65$) and red-flanked duiker ($n = 40$). Camera-traps reveal that red-flanked duiker are only active during the day, which means that their infants are parked while the baboons are awake. Yellow-backed duiker, on the other hand, are predominantly active during the night; thus, mothers will be together with their infants when the baboons stumble across them. However, bushbuck are likewise largely nocturnal. It therefore remains largely unclear why yellow-backed duiker were not preyed upon, as at least their infants fit the same general pattern as the two other antelope prey species.

Conclusions

We provide the first detailed data on predatory behaviour of baboons at a very wet study area in Nigeria with ample vegetation cover that includes forest and tall grass. Some features of meat eating by GGNP baboons resemble those at sites elsewhere. For example, predation is opportunistic, and while it is unknown whether adult males actually catch most prey, they do monopolise most of it; there is no targeted killing bite, and while hangers-on are able to obtain scraps of meat, begging by bystanders or active sharing of meat is absent. Owners of a carcass typically employ evasive tactics, as meat is often aggressively competed over. Still, satiated meat owners sometimes tolerate theft, particularly in the context of male-female and mother-offspring interaction. However, some features are unusual, as this is only the second study site where baboon predation on bushbuck has been observed and the only one for duiker. This atypical prey selection seems to reflect the difficulty of acquiring prey animals outside the usual savannah habitat of baboons, i.e., when vegetation cover is dense and

when potential arboreal prey can find safety in trees. GGNP baboons may therefore be restricted to opportunistic predation on still-lying, parked antelope infants. This could explain why, despite an abundance of other wildlife, predation on large mammals is extremely rare at GGNP. Meat makes up a larger portion of the diet at other baboon sites, although it remains unclear how important this source of nutrition is. In any case, although clearly a desired commodity, mammalian meat is not essential for the survival of baboons at GGNP. Here, the bulk of animal matter is ingested via occasional predation on lizards and the virtually daily consumption of invertebrates.

Our data do not substantiate classic conclusions of the socioecological model that may lead to rather rigid categorisations of animal societies [cf. Dunbar, 1988]. Our findings instead acknowledge intra-specific and intra-generic plasticity within closely related taxa. With this, at least for the predatory behaviour of different baboon populations, we support the model's general prediction that the environment (and not phylogeny or stochasticity) causes behavioural variation.

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CAPTIONS

Table 1. Vertebrate predation by baboons: Overview of reported cases. Numbers refer to individual animals caught. x = predation occurred, but exact number of prey animals unknown; counted as 1 in the summary at the bottom of the table. ? = information not available. Newer scientific species names are used where denotations changed since predation cases were initially reported.

Table 2. Mammals inhabiting baboon study ranges at Gashaka Gumti National Park, Nigeria. Listed are representatives of orders on which baboons elsewhere prey upon. All local species are listed for the orders primates, even-toed ungulates and hares, but only exemplary species for rodents and bats. For details of survey methods on group sizes, see text; nd = no data. Body dimensions from [Kingdon, 2015]. Data on baboons are for comparison only.

Table 3. Predation on forest antelopes by Nigerian baboons. Summary of observed cases.

Fig. 1. Location of Gashaka Gumti National Park in Northeastern Nigeria, West Africa.

Fig. 2. Baboon study sites, indicating home ranges of the crop-raiding troop Gamgam near the village of Gashaka, and the wild-feeding troop Kwano further inside the national park. Research stations are marked by solid circles. (Map design: GJ)

Fig. 3. Baboon prey animal species in the Kwano baboon troop home range. (a) Adult female red-flanked duiker. (b) Adult female bushbuck in riverbed at mineral lick, while baboon troop passes by. (Camera-trap photos: a = Anthony Agbor; b = GJ)

Fig. 4. Baboon troop Kwano – predation on bushbuck infant (2009). (a) AF Mamakane consumes bushbuck carcass on a vine while her daughter and granddaughter are looking on from beneath. (b) AF Mamakane opens up the prey's belly. (Photos: NA)

Fig. 5. Baboon troop Gamgam – predation on red-flanked duiker infant (2012). (a) AM Fedi restrains prey by biting in its rump. (b) AM Fedi restrains prey by grasping around its neck to then kill it by biting through its skull. (Stills from video recorded by JT)

Fig. 6. Baboon troop Kwano – predation on bushbuck infant (2014). (a) AM Erni holds fresh kill in tree. (b) AM Erni bites into belly of carcass. (c) JM Dandi strips flesh from small bone. (d) AM Garrido walks through undergrowth with defleshed carcass. (Photos: ER)