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# Patterns of predation and meat-eating by chacma baboons in an Afromontane environment

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**Abstract –** Meat-eating among non-human primates has been well documented but its prevalence among Afromontane baboons is understudied. In this study we report the predatory and meat-eating behaviours of a habituated group of gray-footed chacma baboons (*Papio ursinus griseipes*) living in an Afromontane environment in South Africa. We calculated a vertebrate-eating rate of 1 every 78.5 hours, increasing to 58.1 hours when unsuccessful predation attempts were included. A key food source was young antelopes, particularly bushbuck (*Tragelaphus scriptus*), which were consumed once every 115 observation hours. Similar to other baboon research sites, predations seemed mostly opportunistic, adult males regularly scrounged and monopolised prey, there was no evidence they used an active kill bite, and active sharing was absent. This is the first baboon study to report predation of rock python (*Python sebae*) eggs and likely scavenging of a leopard (*Panthera pardus*) kill (bushbuck) cached in a tree. We also describe several scramble kleptoparasitism events, tolerating active defence from antelope parents, and the baboons inhibiting public information about predations. In the latter case, baboons with meat often hid beyond the periphery of the group, reducing the likelihood of scrounging by competitors. This often led to prey carcasses being discarded without being fully exploited and potentially providing resources to scavengers. We also highlight the absence of encounters with numerous species, suggesting the baboons are a key component of several species' landscapes of fear. Given these findings it seems likely that their ecological role in the Soutpansberg has been undervalued, and such conclusions may also hold for other baboon populations.

**Keywords –** Afromontane, baboon, meat-eating, monopolisation, predation, scavenging, scrounger.

## Introduction

Many wild non-human primate species have diverse and highly flexible diets (Chapman and Chapman, 1990), and although most species are heavily reliant on plant derived food items, animal matter from invertebrates is consumed quite regularly (Cassalett and Rothman, 2018). Vertebrate meat-eating, although less frequent, has also been observed in at least 89 species of non-human primates (Watts, 2020). Examples include, *Cercopithecus* monkeys predating on galagos (Butynski, 1982), flying squirrels (Fairgrieve, 1997), and bats (Tapanes et al., 2016); Japanese macaques (*Macaca fuscata*

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*yakui*) on frogs and lizards (Suzuki et al., 1990); snub-nosed monkeys (*Rhinopithehcus bieti*) on birds and squirrels (Ren et al., 2010); and Cebinae monkeys on lizards, bats, squirrels (Fedigan, 1990), snakes (Falótico et al., 2018), and coati (Newcomer and De Farcy, 2016; Fedigan, 1990).

Predatory behaviours have also been observed in larger-bodied species, most notably on young antelopes by mandrills (*Mandrillus sphinx*) (Kudo and Mitani, 1985) but are also widespread across all *Papio* species (Strum, 1975; Hausfater, 1976; Davies and Cowlishaw, 1996; Goffe and Fischer, 2016; Sommer et al., 2016; Schreier et al., 2019). Bonobos (*Pan paniscus*) are able to predate mature duiker (*Cephalophus monticola*, *C. dorsalis*, and *C. nigrifrons*) (Hohmann and Fruth, 2008), whilst chimpanzees (*Pan troglodytes*) prey on antelope (*C. monticola* and *C. callipygus*) and bushpig (*Potamochoerus porcus*) (Mitani and Watts, 1999), with predation on smaller monkey species such as red colobus (*Piliocolobus badius*) (Mitani and Watts, 1999) receiving significant attention. Bonobos have also been observed preying on smaller primates (*Cercopithecus ascanius* and *C. wolfi*) (Surbeck and Hohmann, 2008) and baboons are known to prey on vervets (*Chlorocebus pygerythrus*) (Hausfater, 1976) and mangabeys (*Cercocebus galeritus*) (Kivai, 2013).

Carnivorous behaviours have been observed on a range of prey across all *Papio* species (Sommer et al., 2016), with consumption of animal matter reported in almost all populations (Hill and Dunbar, 2002). Nevertheless, most reports of baboon predatory behaviour have come from ‘open’ habitats (such as grassland, farmland etc), with fewer observations from forest habitats (Sommer et al., 2016). We add to these observations by describing the predation and vertebrate meat-eating behaviours of a habituated group of gray-footed chacma baboons (*Papio ursinus griseipes*) living in the Soutpansberg Mountains, South Africa. This study group inhabited a complex mosaic of habitats within a mountainous environment (Willems and Hill, 2009) collectively belonging to Afromontane mist-belt communities (Coleman and Hill, 2014a). We detail the diversity of prey species captured, the capture methods, and animal matter consumed and discarded. We also highlight seasonal trends in antelope predation and the interactions the study group had with other species. As such, this report provides new insights into the behaviours of baboons living in these ecosystems and we discuss the impacts these predatory behaviours may have on local ecological communities.

Chacma baboons live in multi-male multi-female groups with females holding relatively stable linear hierarchies, whilst male hierarchies often fluctuate between stable and unstable structures. Although meat sharing has been reported in Guinea baboons (*P. papio*) (Goffe and Fischer, 2016), chacma (*P. ursinus*), yellow (*P. cynocephalus*), and olive (*P. anubis*) baboon males typically monopolise prey and discard once achieving satiation, allowing sequential feeding by other individuals (Hausfater, 1976; Hamilton III and Busse, 1982; Sommer et al., 2016). Here, we recorded the identity of the baboons at numerous events and thus offer insights into the role of dominance rank and clique membership in affording access to vertebrate meat, and how changes in rank stability can alter patterns of conflict during meat-eating.

## Methods

### STUDY AREA

All observational data were collected on a wild habituated group of chacma baboons (*Papio ursinus griseipes*) in the western Soutpansberg Mountains, South Africa (S29.44031°, E23.02217°) between February 2014 and July 2019. The majority of the study area was classified as a private nature reserve; however, some land clearance had taken place for agricultural purposes within the study group’s core area (Williams et al., 2017). This region experiences pronounced wet and dry seasons (Mostert et al., 2008). Though much of 2015 and 2016 were in drought conditions, whilst the latter stages of 2017 experienced lower rainfall than expected.

### STUDY GROUP

Although chacma baboons are not forest specialists, the study group often utilised these habitats due to their proximity to sleeping cliffs and the food items within them. The baboons consumed a wide variety of food items from a diverse range of habitats, giving them dietary overlap with forest- and savannah-dwelling species. In 2015 the group contained approximately 70 individuals and grew to 92 individuals by the end of the study. This increase was mostly from births as only three permanent immigrations occurred, and there were few confirmed mortalities or disappearances.

The study group was habituated circa 2005 and was the focus of intermittent research attention until 2014. From 2007 onwards numerous researchers collected data on the study group via direct observations (e.g., Howlett et al., 2015; de Raad and Hill, 2019; Allan and Hill, 2021; Allan et al., 2021), indicating that habituation was at the level typically found in study groups elsewhere. From 2014, we conducted follows from dawn until dusk (i.e., full day) 3 to 4 days a week, with occasional gaps of up to 5 weeks in duration. This follow schedule was designed so that the study group retained as much of their natural interactions with predators as possible by ensuring the baboons spent significant time without observers who may influence the frequency and nature of predator-prey interactions (LaBarge et al., 2020b).

### VERTEBRATE ANIMALS IN STUDY AREA

Domestic livestock were not common in the study area, but part of the groups' home range included a small cattle herd. The study group was frequently observed staring into a chicken coop on a farm and occasionally attempted to gain access. Domestic dogs and cats were also present in parts of the baboon's home range. Whilst cats were rarely observed in proximity to the baboons and we never saw them being chased or receiving agonism from the baboons either, the baboon's seemed to consider the dogs threatening (usually alarm called and fled) and did not appear to threaten them, contrary to observations from elsewhere (Sommer et al., 2016).

The density of the various vertebrate species occupying the study area was not known for the observation period but a scat analysis of brown hyena and leopard diets (Williams et al., 2018) may reflect some relative density information for certain prey species. We recorded all encounters this habituated baboon group had with other species and noted the behaviours and response of each species during the encounters. We considered encounters as anytime at least one baboon was within 10 meters of another species (whether interacting or not), however, active encounters involving alarm calls were also recorded despite the threatening animal often not being within 10 meters of any of the baboons (e.g., crowned eagles and leopards).

## Results

### ENCOUNTERS WITH OTHER SPECIES

We observed 917 interactions between the baboons and other species (see table 1), of which 673 were considered passive (i.e., neither species appeared to alter their behaviour). The baboons were observed scrounging from (supplanting from a food patch) or displacing the other species on 16 occasions and were themselves scrounged from or displaced 24 times. Baboons were startled (i.e., flinching and running away a few meters) on 74 occasions, mostly by adult bushbuck (n = 24), warthog (n = 21), and bushpig (n = 8). In 18 encounters we observed the other species alarm call, flee, or evade the baboons, whilst we also observed the baboons alarm on 18 occasions (n = 10 for leopards). Finally, we observed the baboons acting aggressively towards the other species (e.g., chasing, attacking, threat gestures/vocalisations) on 38 occasions, however most of these were directed towards samango monkeys (n = 34) and leopards (n = 8, all during alarm events).

### PREY SPECIES AND SEASONALITY

Between January 2014 and July 2019 (373 observation days) the study group was observed eating vertebrate animals on 57 occasions, including two scavenging events (table 2). Discounting scavenging events, baboons preyed on

**Table 1.** Frequency of encounters between baboons and other animals occupying the study area. Passive encounters were when neither species appeared to alter their behaviour according to the presence of the other within 10 meters. Playing occurred between juvenile baboons and juveniles of the other species. Some observations were missing detailed notes, in these cases the sum of each encounter type does not equal the total number of encounters. *Baboons startled by alarm calls made by the samango monkeys. †Baboons mobbed the leopard after it predated on an adult male baboon from the group. ††All 3 observations were from an unhabituated baboon group.

| Species | Total | Passive encounters | Playing | Baboons displaced/ scrounged from | Baboons startled | Baboons received charge/ aggression | Baboons alarm called | Baboons scrounge/ displace prey animal | Baboons aggressive towards other spp | Other spp alarm, flee, or evade |
|---|---|---|---|---|---|---|---|---|---|---|
| **Birds** | | | | | | | | | | |
| Adult hadada ibis, Bosttrychia hagedash | 13 | 9 | | | 4 | | | | | |
| Crested guinea fowl, Guttera pucherani | 2 | 0 | | | | | | | 0 | 1 |
| Francolin, Dendroperdix sephaena | 8 | 0 | | | | | | | | 1 |
| Speckled pigeon, Columba guinea | 1 | | | | 1 | | | | | |
| **Small mammals (1-15 kg)** | 0 | | | | | | | | | |
| Banded mongoose, Mungos mungo | 6 | 1 | | | | | | | | 4 |
| Bush squirrel, Paraxerus spp | 1 | | | | | | | | | 1 |
| Juvenile bushbuck, Tragelaphus scriptus | 11 | 4 | | | | | | 2 | | 2 |
| Cape porcupine, Hystrix africaeaustralis | 1 | 1 | | | | | | | | |
| Dwarf mongoose, Helogale parvula | 2 | 1 | | | | | | | | 1 |
| Gambian giant rat, Cricetomys gambianus | 0 | | | | | | | | | |
| Adult klipspringer, Oreotragus oreotragus | 33 | 26 | | | 4 | 1 | | 2 | | |
| Adult klipspringer with young | 1 | 1 | | | | | | | | |

**Table 1.** (Continued.)

| Species | Total | Passive encounters | Playing | Baboons displaced/ scrounged from | Baboons startled | Baboons received charge/ aggression | Baboons alarm called | Baboons scrounge/ displace prey animal | Baboons aggressive towards other spp | Other spp alarm, flee, or evade |
|---|---|---|---|---|---|---|---|---|---|---|
| Large spotted genet, Genetta maculata | 2 | | | | | | | | | 2 |
| Lesser bushbaby, Galago moholi | 0 | 0 | | | | | | | 0 | |
| Adult red duiker, Cephalophus natalensis | 16 | 13 | | | 3 | | | | | |
| Juvenile red duiker | 0 | | | | | | | | | |
| Rock dassie, Procavia capensis | 5 | 3 | | | | | | | | 2* |
| Habituated samango groups, Cercopithecus albogularis schwarzi | 190 | 154 | 13 | 4 | 5* | | | 7 | 19 | 1 |
| Habituated bachelor samango | 138 | 111 | | 7 | 2* | | | 2 | 15 | 1 |
| Unhabituated samango monkeys | 0 | | | | | | | | | |
| Scrub hare, Lepus saxatilis | 2 | 0 | | | | | | | 0 | 1 |
| Sharpe's grysbok, Raphicerus sharpei | 0 | 0 | | | | | | | 0 | |
| Slender mongoose, Galerella sanguinea | 1 | | | | | | | | | 1 |
| Steenbok, Raphicerus campestris | 0 | 0 | | | | | | | 0 | |
| Thick-tailed bushbaby, Otolemur crassicaudatus | 1 | 0 | | | | | | | 0 | |
| Vervet, Chlorocebus pygerythrus | $3^{\dagger\dagger}$ | 0 | | | | | | | | $3^{\dagger\dagger}$ |

**Table 1.** (Continued.)

| Species | Total | Passive encounters | Playing | Baboons displaced/ scrounged from | Baboons startled | Baboons received charge/ aggression | Baboons alarm called | Baboons scrounge/ displace prey animal | Baboons aggressive towards other spp | Other spp alarm, flee, or evade |
|---|---|---|---|---|---|---|---|---|---|---|
| **Medium mammals (16-50 kg)** | 0 | | | | | | | | | |
| Adult/subadult bushbuck | 239 | 202 | | 6 | 24 | 2 | 1 | 2 | 1 | 1 |
| Adult bushbuck with young | 8 | 2 | | 1 | 1 | 2 | | | 1 | |
| Adult common warthog, Phacochoerus africanus | 48 | 34 | | 1 | 12 | 1 | | | | |
| Warthog group with juveniles | 48 | 35 | | 2 | 9 | 1 | | 1 | | |
| Adult Bushpig, Potamochoerus larvatus | 8 | 1 | | | 7 | | | | | |
| Bushpig group with juveniles | 2 | | 1 | | 1 | | | | | |
| Adult common duiker, Sylvicapra grimmia | 6 | 6 | | | | | | | 0 | |
| Grey rhebok, Pelea capreolus | 4 | 4 | | | | | | | | |
| **Large mammals** (> **50 kg)** | 0 | | | | | | | | | |
| Adult Greater kudu with juveniles | 4 | 2 | | | 2 | | | | | |
| Adult Greater kudu, Tragelaphus strepsiceros | 15 | 12 | | | 3 | | | | | |
| Blue wildebeest group, Connochaetes taurinus | 1 | 1 | | | | | | | | |
| Giraffe, Giraffa camelopardalis | 4 | 4 | | | | | | | | |
| Waterbuck, Kobus ellipsiprymnus | 3 | 1 | | | 2 | | | | | |
| Zebra group, Equus quagga | 2 | 2 | | | | | | | | |

**Table 1.** (Continued.)

| Species | Total | Passive encounters | Playing | Baboons displaced/ scrounged from | Baboons startled | Baboons received charge/ aggression | Baboons alarm called | Baboons scrounge/ displace prey animal | Baboons aggressive towards other spp | Other spp alarm, flee, or evade |
|---|---|---|---|---|---|---|---|---|---|---|
| **Herpetofauna** | 0 | | | | | | | | | |
| Leopard tortoise, Stigmochelys pardalis | 12 | 7 | 2 | 3 | | | | | | |
| Giant plated lizard, Gerrhosaurus validus | 1 | 1 | | | | | | | | |
| Spotted bush snake, Philothamnus semivariegatus | 1 | 1 | | | | | | | | |
| **Predators (of all baboon age-sex classes)** | 0 | | | | | | | | | |
| Leopard, Panthera pardus | 10 | | | | | | 10 | | 8$^{\dagger}$ (all during alarms) | |
| **Predators (of baboon juveniles & infants)** | 0 | | | | | | | | | |
| Crowned eagle, Stephanoaetus coronatus | 21 | 17 | | | 1 | | 2 | | 1 | |
| Brown hyena, Hyaena brunnea | 1 | | | | | | 1 | | | |
| African rock python, Python sebae | 7 | 3 | | | | | 4 | | | |
| African harrier-hawk, Polyboroides typus | 5 | 3 | | | 1 | | 1 | | | |
| Honey badger, Mellivora capensis | 2 | | | | | | 2 | | 2 (during alarms) | |
| Verreaux’s eagle, Aquila verreauxii | 4 | 3 | | | | | 1 | | | |
| Black sparrowhawk, Accipiter melanoleucus | 2 | | | | 1 | | | | 1 | |
| Kestrel, Falco rupicolus | 1 | | | | 1 | | | | | |

**Table 1.** (Continued.)

| Species | Total | Passive encounters | Playing | Baboons displaced/ scrounged from | Baboons startled | Baboons received charge/ aggression | Baboons alarm called | Baboons scrounge/ displace prey animal | Baboons aggressive towards other spp | Other spp alarm, flee, or evade |
|---|---|---|---|---|---|---|---|---|---|---|
| **Other potential threatening species** | 0 | | | | | | | | | |
| Cape vulture, Gyps coprotheres | 1 | | | | 1 | | | | | |
| White necked raven, Corvus albicollis | 5 | 4 | | | | | 1 | | | |
| Unknown raptor spp | 1 | | | | 1 | | | | | |
| Mozambique spitting cobra, Naja mossambica | 1 | | | | | | 1 | | | |
| Snouted cobra, Naja annulifera | 2 | 2 | | | | | | | | |
| Puff adder, Bitis arietans | 1 | | | | | | 1 | | | |
| Unknown snake | 2 | 2 | | | | | | | | |

**Table 2.** Summary of predations on vertebrate animals by the study group. Two cases of scavenging are recorded as "+1" in table, as these may not be considered true predations. Numbers in parentheses indicate the number of failed attempts predating on prey species. Calendar months and dry/wet season information included to highlight seasonal trends in predatory behaviour.

| | Jan | Feb | Mar | Apr | May | Jun | Jul | Sep | Oct | Nov | Dec | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Wet | Wet | Wet | W/D | Dry | Dry | Dry | Dry | D/W | Wet | Wet | |
| Antelope spp | | | | | | 1 | | | | 2 | | 3 |
| Banded mongoose | | | | (1) | | | | | | | | (1) |
| Bushbaby | | 1 | | | | | | | | | | 1 |
| Bushbuck | 1(1) | | 5 + 1 | 1 (1) | 6 | 5 (1) | 2 | 1 | 1 | 2 | 1 | 25 + 1 (3) |
| Rock dassie | | | | | (1) | | 1 + 1 | | | | | 1 + 1 (1) |
| Francolin | | | 2 (3) | 1 | | | | | | (1) | | 3 (4) |
| Crested guineafowl | | | | | | | | | | (1) | | 0 (1) |
| Klipspringer | 1 | | (1) | 1 | | | | | | | | 2 (1) |
| Red duiker | 1 | | 3 | (1) | (2) | | 4(1) | | 1 (1) | | (2) | 9 (7) |
| Scrub hare | | | | | | | | | | (1) | | 0 (1) |
| Rodent | | 1 | 1 | | | | | | 1 | | | 3 |
| Skink | | | 1 | | | | | | 1 | 1 | 1 | 4 |
| Small bird | | 2 | (1) | 1 | | | | | 1 | | | 4 (1) |
| **Total** | **3(1)** | **4** | **13 (4)** | **4 (2)** | **6 (2)** | **6 (1)** | **8(1)** | **1** | **5 (1)** | **5 (3)** | **2** | **55 + 2 (20)** |

vertebrate animals at a rate of one every 6.8 days or 81.6 observations hours (using 12 hours as the average day length). We also observed 20 failed predation attempts across a range of species (see table 2). Combined with successful events this means the group made attempts to predate and consume vertebrates at a rate of one every 4.97 days or 59.7 hours. Antelope species made up 39 of the 55 (70.1%) predation episodes at a rate of one every 9.56 days/114.8 hours (excluding one scavenging event), with eleven additional failed attempts, yielding an overall antelope predation attempt rate of one every 7.46 days/89.5 hours.

Successful bushbuck predations occurred 11 times on both fawns and small juveniles (coordinated and able to run, likely $< 10$ kg bodyweight). Neonates were predated twice and larger juveniles (likely $> 10$ kg) once. Unsuccessful bushbuck predations were on larger juveniles, who either dodged attacks ($n = 1$) or withstood the initial attack by baboons before kicking free ($n = 2$). All successful red duiker predations were on juveniles ($n = 5$) and fawns ($n = 4$), whilst unsuccessful attempts occurred on adults ($n = 3$), subadults ($n = 2$), and juveniles ($n = 2$). Although red duikers are a small antelope (adults approximately 10 kg), they are agile and fast, making it challenging for the baboons to pin them down and mortally wound them. Successful klipspringer predations were on a fawn and a juvenile, with an unsuccessful attempt on another juvenile that was too quick for the baboons to chase down.

There were two occasions of baboons eating eggs, one event was confirmed to be small bird eggs, whilst the other event was likely rock python. In the latter case, a group of baboons discovered a batch of large eggs (each approx. 8–10 centimeters) in diameter. There were 7 eggs remaining upon our arrival, but aggressions in the area alerted us to the event, suggesting more had already been taken. In both observations the baboons appeared adept at consuming the contents of the eggs, indicating they were not novel items.

### CAPTURE METHODS AND KILL METHODS

We observed the capture method for successful predation events 33 times. Consistent across all species of prey, the baboons typically lunged and grabbed the animal before pinning it down and biting it. Baboons did not appear to use a kill bite as consumption often began before the prey animal had died, with rodents, francolin, dassie, and antelope, usually bitten several times before dying. With antelope, the baboons were frequently observed biting the abdomen of the prey initially, which opened the body cavity and allowed access the internal organs.

An adult male (ID: DAV) was observed searching deep inside rock crevices with his hands attempting to capture an adult female dassie with an infant. Several juvenile baboons observed the adult baboon's behaviour, and mimicked predation attempts once the male moved away, but all were unsuccessful.

Francolin and small birds (n = 4, n = 3) were captured directly from nests or bushes, typically by juveniles (one by an adult male). When francolin were able to detect the baboons early, they would alarm call and fly beyond the periphery of the group (n = 3); in these scenarios the baboons chased the birds and attempted to grab them from the air.

Baboons chased down juvenile antelope on 4 occasions. One event occurred across an open area where an adult male (ID: DAV) detected an adult klipspringer with a juvenile, the adult male baboon chased the juvenile klipspringer for over 100 meters before it tired and was caught by the baboon. Although the group probably make kills regularly by uncovering young antelope 'parked' in long-grass (see Sommer et al., 2016), this was only directly observed on one occasion by an adult female during the study period, although had been observed frequently prior to 2014 (pers. obs.). One additional bushbuck feeding event came after an adolescent male was observed climbing into a tree and returning to the ground with a bushbuck corpse (bigger than normally observed for predations by this group), likely a case of scavenging a cached kill from a leopard. The group encountered aggressive defence from adult antelopes on two occasions; the baboons seemed fearful of the adults (fleeing and alarm calling) yet managed to successfully evade the adults and predate the fawns in both cases.

Finally, on five occasions prey was captured when several individuals were in proximity, leading to scramble kleptoparasitism, whereby the prey animal was bitten/consumed concurrently by several individuals (max 9 observed). In four of these cases the carcass was eventually torn apart into smaller monopolisable sections. For 11 antelope meat-eating events we arrived with a monopolising male surrounded by several individuals chewing meat, these individuals were usually members of the dominant female clique (NOR = 7, MAN = 6, ATH = 2); however, the dominant (NOR) female's juvenile sons were also observed (n = 2), and other adult males (n = 6).

### SOCIAL DYNAMICS DURING MEAT EATING

Across all prey species, the age-sex class of the predatory baboon was identified 34 times, including during scramble kleptoparasitism events (adult/adolescent males = 15, adult/adolescent females = 9, juveniles = 10). For antelope specific events (not including scramble episodes), we observed males predating most often (n = 8), but female (n = 5), and juvenile (n = 2) capture events were also observed. Monopolisation of prey items (i.e., one animal being the sole consumer of an entire animal or part of an animal for at least several minutes) was observed in 52 of 57 meat-eating events. Across all prey items, monopolisation occurred after an animal scrounged the meat (i.e., took it from another baboon) 17 times, 12 of which were on antelope carcasses. The latter was likely more frequent given we missed the predation event on several occasions and identified several individuals already chewing meat in proximity to a monopolising adult male upon our arrival. In 11 cases (10 for antelopes) conflict over the corpse led to multiple monopolisation events.

Monopolisation could be achieved by fleeing with the prey beyond the periphery of the group (non-antelope = 9, antelope = 9). Only adult and adolescent males were observed scrounging and monopolising the discarded carcasses (n = 9). 'Begging' was not observed and there were no attempts by subordinate individuals to groom the monopolising male to gain access (Sommer et al., 2016). Instead, it was common to observe numerous individuals congregating around the monopoliser and watching from a distance, potentially queuing or exhibiting a 'vulture response' (Altmann and Altmann, 1970; Sommer et al., 2016). Across all events 37 individuals were observed behaving this way within 5 meters of the monopolising male. Across all events we recorded 19 non-monopolising individuals acquiring scraps, either through inspecting the area after the monopoliser moved, picking up scraps that fell as the monopoliser moved, or 'stealing' scraps whilst the monopoliser was distracted.

Two non-dominant adult females (SIL = 1, MEL = 2) who shared strong affiliative bonds with the monopolising male (FLE = 2, NAT = 1) (due to prior or ongoing consortships) were able to secure scraps without receiving aggression. These instances were also the only time these females were observed consuming meat. Interestingly, in all three of these events the scraps were within an arm's reach of the monopolising male, and he did not appear distracted by any external threats, these co-feeding events therefore match the definition of passive meat-sharing presented by Goffe and Fischer (2016). This was never observed with the other males who often threatened or fought with the dominant females despite typically being strong associates at the time. The dominant female (ID: NOR) was often seen grimacing, gecking, and barking at the monopolising males. She made similar vocalisations (albeit less aggressively) when displaced by dominant males (outside of predation scenarios), observers (Allan et al., 2020), or larger bodied mammals such as cows and warthogs.

Across a 3-year period (2014–2016) the male baboons had a relatively stable hierarchy, and in 2015 and 2016 there was a clear dominant male (ID: DAV) who monopolised 12 (8 scrounged) out of 17 antelope carcasses (although this is likely higher because identity wasn't recorded on 4 occasions). In this period, DAV was frequently surrounded by the remaining males whilst he consumed meat. Despite the proximity and threatening gestures made by the other males, the dominant individual rarely moved and only two aggressions were observed concurrent to predation events between 2014 and 2016; neither were towards the dominant male. Although the dominant male tolerated proximity from the dominant females (ID: NOR, MAN, ATH), they were not observed gaining access to scraps once the male had monopolised the carcass, despite being frequent consort partners.

Throughout 2017 to 2019, 15 of 19 meat-eating episodes were associated with at least one aggression within the group and included 22 monopolisation episodes by males (FLE: 7, DAV: 5, BLO: 4. EGO: 2, GOR: 1, JOS: 1, NAT: 1), with 2 events where the carcass was ripped apart into smaller pieces. During this period, the hierarchy had become unstable with rank positions fluctuating regularly. Despite, monopolisation typically being achieved by the most dominant or aggressive individuals we also observed the lowest ranked male (ID: JOS) monopolise a carcass scrounged from another male (ID: DAV, who seemed to discard very early to prioritise mate-guarding). The low ranked male was initially threatened by three higher-ranking individuals, but he aggressively defended the carcass (very rare for this individual to show any resistance to higher-ranked individuals) and was able to evade attention by moving beyond the periphery of the group.

### ANIMAL MATTER CONSUMED AND DISCARDED

In total we observed 33 discarding events across all species. In the 4 skink predations the tail was always discarded, and on 3 occasions the lower limbs were also discarded. When meat was consumed from francolin or other bird species the baboons always discarded feathers. Eating meat from birds could often be very selective, with small amounts of muscle tissue eaten and a lot of the animal's intact carcass discarded (n = 7). One adult male (ID: DAV) was observed consuming large amounts of the flesh, muscle tissue, and organs from a francolin, but most of the bones were discarded with minor amounts of muscle tissue still attached. The capture of a bushbaby was not observed, but an adult male (ID: DAV) was seen chewing on the animal (full cheek pouches) and biting pieces of flesh off of a bushbaby arm. No discarded material was identified from rodent or bushbaby predation events.

During the single predation event on a dassie, the adult male (ID: DAV) discarded the intestinal tract after inspecting and sniffing it and avoided eating the stomach by moving it aside whilst accessing other parts of the carcass. We also found a dead dassie one morning before the baboons climbed up from their sleeping cliff; rigor mortis was already apparent, with no marks indicating cause of death. An adult male (ID: JOS) initially groomed the carcass, potentially consuming external parasites, before beginning to consume meat shortly after. Most of the scavenged dassie was discarded after two lower-ranking adult males (ID: JOS and NOS) repeatedly sniffed and bit the corpse, suggesting it may have been rancid.

Early stages of antelope consumption appeared to focus on viscera, followed by the gluteal and upper hindlimb muscles. Smaller muscle groups were usually taken later along with chewing and swallowing large amounts of the femur (see fig. 1a). Bone chewing seemed largely restricted to when monopolisers discarded remains in proximity to other baboons. In all antelope eating events, attempts were made by all of the males to bite open the skull to consume brain matter (usually after other parts of the carcass) and was observed in this study group in 2012 (ID: PIN, see fig. 1b). During this study, one individual (ID: DAV) consistently managed to bite open the skull and consume brain material (6 confirmed observations) whilst only one other individual (ID: EGO) was once observed eating the brain mass of a young fawn.

The baboons were observed dropping or discarding animal matter during 23 of the 40 antelope-eating events. Discarded material would typically include the fur/skin attached to leg bones and hooves, with minor amounts of muscles and connective tissue remaining (observed 8 occasions, plus 1 from camera-traps). Discarding of large amounts of the carcass was always facilitated by a monopoliser successfully evading competitors beyond the periphery of the group. As such, the discarded remains were not exploited by other group members (n = 8), though it was often challenging to maintain proximity in thick bush, so the outcome was unknown for most events.

**Figure 1.** Baboon predation on bushbuck (*Tragelaphus scriptus*) at Lajuma in 2012. Most of the viscera was consumed during a scramble episode at the beginning of the predation event, but an adult male (MRS) successfully monopolised the kill and evaded competitors beyond the periphery of the group. a) MRS consuming large amounts of muscle tissue and bone. Two adult males (DAV and PIN) gained access to the carcass after MRS had discarded. b) PIN biting into the skull to access brain material, he also consumed the eyes and tongue. Despite the sequential feeding of the carcass the intestines were actively avoided. PIN was not in the group during this study (2014–2019). Photos: CH 2012.

**Figure 2.** Camera-trap images of a) adult male baboon (ID: NAT) consuming meat from bushbuck fawn, b) common genet consuming bushbuck meat, c) African civet dragging remains away, and d) thick-tailed bushbaby inspecting the area on the subsequent evening. The times on the camera-trap were incorrectly set to 12h format, thus AM times should be PM and vice versa.

During two of the scramble events the prey carcass was split into several pieces, and, while the same items were still discarded, they were scattered around. Scattering could also happen in non-scramble events due to aggression (n = 5), monopolisers or sequential feeders moving locations after discarding elements of the carcass (n = 12), and individual's eating prey in trees which facilitated scraps to fall to the ground (n = 3). Many of these outcomes could happen during a single predation event. On one occasion an adolescent male discarded parts of intestinal tract that two infants later played with and consumed.

One antelope meat-eating episode was captured on a camera-trap (see fig. 2). This occurred when the group was not followed, but camera-trap images showed an adult male (ID: EGO) consuming meat and discarding it with muscle tissue remaining and the head, legs, and hooves intact. A second male (ID: NAT) then consumed some of the remains but discarded the rest shortly after failing to break open the skull. That evening the corpse was fed on by at least one common genet (*Genetta genetta*), before an African civet (*Civetticitis civetta*) later removed the carcass. On the subsequent night genet, civet, and thick-tailed bushbabies (*Otolemur crassicaudatus*) were captured inspecting the area where the carcass had been.

## NOTABLE ABSENCES

In a 4.5-year period there was an absence of interactions (i.e., another species observed within 10 meters of at least one baboon), or aggressive/predation encounters between the habituated baboon group and crested guinea fowl, vervet monkeys, and bushbabies (*O. crassicaudatus* and *Galago moholi* at the field site). While the latter are nocturnal, they were observed interacting with vervets during the daytime at the same field site. Encounters between the baboons and mongoose species were also minimal (n = 9, see table 1), six of which produced alarm and flee responses from the mongoose, including one predation attempt by a juvenile baboon. Red rock dassie occur abundantly across the baboon's home range, but they were rarely observed within 10 meters of the baboons, with three passive encounters, one eliciting dassie alarm calls, and one encounter where juvenile baboons chased the dassie (which may have been a predation attempt). On multiple occasions dassie alarm calls were heard, but visual observations were not made.

## Discussion

Although the chacma baboon study group consumed eggs, birds, and lizards, mammals were most common, particularly young antelope. We calculated an antelope predation rate of one every 9.56 days, which is approximately one every 115 hours (using 12 hours as the average day length), with vertebrate eating-episodes taking place every 78.5 h (including all species and scavenging), increasing to 58.1 h when all unsuccessful attempts are included. This rate is far higher than the reported rate of 1291 h for olive baboons living in forests in Gashaka Gumti National Park (Sommer et al., 2016), although mammal predation rates as low as every 12 h (25 h for antelope) have been reported for olive baboons near Gilgil, Kenya (Strum, 1975). The latter is likely due to greater opportunities as antelope species present at higher densities near Gilgil compared to the Soutpansberg. Nevertheless, our findings demonstrate that vertebrate (and particularly mammalian) meat represent an important part of the study group's diet and is higher than has been observed in many other baboon groups.

### SAMPLING ISSUES

Our observations suggest the study group rarely consumes smaller mammalian prey such as rodents or leporids, with non-mammalian vertebrate prey such as eggs, birds, and lizards also observed less frequently than antelope. This is similar to observations on olive baboons by Sommer et al. (2016); although a number of sampling issues are important to consider which may underrepresent predation data at our site. Dense vegetation and a mountainous terrain likely meant many predations on smaller species and eggs were not observed. Indeed, the few observations we made were typically 'chance' observations as they were not accompanied by the easily recognisable sounds of antelope predations (i.e., screaming of prey) or agonistic episodes within the group. It was also challenging for observers to detect events given the carcass holders were adept at fleeing into dense bush or beyond the periphery of the group. The speed of consumption also made it difficult to identify and record predations on lizards as baboons could identify, grab, and consume the animals in a matter of seconds. This suggests observers would be unlikely to witness it on a consistent basis unless the study was focused on collecting data on vertebrate predation or precise foraging behaviours; as a result, observers are not primed to detect these events.

### POSSIBLE UNDERREPRESENTED PREY SPECIES

Encounters with francolin (n = 8) almost always resulted in predation attempts by our study group, usually initiated by juvenile baboons in peripheral locations. Elsewhere, gray-footed chacma baboons prey on helmeted guinea fowl (*Numida meleagris*) (Branch, 2017), yet we observed only one encounter between the baboons and guinea fowl (a predation attempt by juveniles). From mid-2015 onwards, several groups of guinea fowls were habituated by local researchers who communicated that alarm and flee/evade behaviours were displayed consistently by the guinea fowl upon hearing baboons in the area (often more than 100 meters away), suggesting guinea fowl perceive a risk from the baboons.

During the study period, we monitored a group of habituated vervets who also exhibited similar alarm and evade behaviours when baboons were heard in the wider area. Confirmed cases of vervet predation by baboons have occurred at Lajuma (Willems and Hill, 2009) but was not observed during our study period, although unhabituated baboon groups were observed chasing vervets three times during the study period (all accompanied by aggressive grunting and screaming by the baboons and alarm calls from the vervets). These factors may suggest that baboons continue to prey on the vervets at Lajuma as observed elsewhere (DeVore and Washburn, 1963; Hausfater, 1976; Hamilton III and Busse, 1982; Fichtel, 2012), although as with guinea fowl the vervets appear to minimise the possibility of encountering baboons which impacts on their patterns of space use (Willems and Hill, 2009).

Considering the study group likely continues to predate on vervets, it is curious that observations of baboons predating on samangos are completely absent at this field site over a 15-year period. There were two habituated groups of samangos (one of approx. 40 individuals, another of approx. 70) that the baboons often encountered and spent time in proximity to. We observed producer-scrounger dynamics, playing between juveniles, and aggressions between varying age-sex classes (including redirected aggression) between the two species, all of which showed considerable similarities to intraspecific baboon behaviours. We also frequently observed low-ranked adult and adolescent female baboons and juvenile baboons (of both sexes) attempting to attack adult and subadult male samangos without provocation (table 1). These observations suggest a nuanced social dynamic between the two species, which may factor into the absence of predatory behaviours.

The presence of a large adult male samango (and multiple males during breeding seasons) may also be a possible reason for a lack of predation attempts. Samangos of varying age-sex classes are also known to aggressively defend areas of their home ranges (LaBarge et al., 2020a), suggesting baboons could be wary of instigating conflict with large groups, which were large compared to study groups elsewhere (Coleman and Hill, 2014b). It is possible that baboons predate upon unhabituated samango monkeys but interactions with unhabituated samango groups were absent, likely due to observers displacing them (LaBarge et al., 2020b). Although the risk of mobbing would likely be lower in these scenarios given that unhabituated groups had substantially lower group-sizes, there is no observational evidence to suggest this has occurred in the study area. Given the baboons are adept climbers at Lajuma, the samangos likely would not have been able to avoid predation by climbing into tall trees, contrary to observations elsewhere (Sommer et al., 2016).

Interactions between leopard tortoises (*Stigmochelys pardalis*) and baboons were also observed (n = 12) and older individuals often displaced away from the tortoise if they moved. On two separate occasions juveniles were observed sniffing and playing with tortoises, but the contact did not lead to predation attempts, in contrast to observations from other field sites (Hill, 1999). Leopard tortoises are larger than the angulate tortoises predated in the Western Cape (Hill, 1999) however, and their size and carapace thickness may be sufficient to prevent predation from baboons. Equally, despite being native to South Africa, the leopard tortoises were introduced to Lajuma in the prior decades, thus the baboons may not have learned how to access the protective carapace yet.

Although the baboons frequently shared passive encounters with adult warthog accompanied by juvenile offspring (table 1), no attempts were made to predate the juveniles. The baboons were startled away by bushpig and warthog frequently (table 1), suggesting the baboons perceived even young *Suidae* to be too risky to prey upon due to aggressive defence by adult animals (Sommer et al., 2016).

It is likely that predations occur on non-juvenile red duikers although only three unsuccessful attempts on adult red duiker were observed. Despite this, adult red duiker were occasionally observed foraging near the baboons and could startle the baboons if they moved quickly (table 1). We did not observe the baboons having a non-predation encounter with lone juvenile red duiker or klipspringer. Adult bushbuck with juveniles (that are approximately the same height as the baboons (likely $>10$ kg bodyweight)) did not receive predation attempts, but adults with young were rarely encountered by the baboons for any antelope species (table 1). Sharpe's grysbok, steenbok, and common duiker were also identified within the baboon's typical home range, but only the latter was observed within proximity of a baboon (n = 6, all adults) and none received any predation attempts.

Collectively, these observations (and lack thereof) suggest that there may be a critical body size limit for prey animals, with baboons avoiding prey that are too large to be captured safely. Similar findings have been reported for chimpanzees (Bugir et al., 2021). An awareness of mobbing risks or collective defence from gregarious species may also render predation attempts too great of a risk. Interestingly, the baboons exhibited an ability to tolerate risk of injury when attempting to predate aggressively defended fawns of bushbuck and klipspringer. Thus, the baboon's perception of whether an animal is prey, or a potential threat may be a combination of learning (personal or social) and innate selective processes as hypothesized and shown in other predator-prey systems (Lindstrom et al., 1999; Exnerová et al., 2007; Sherratt, 2011; Hämäläinen et al., 2021).

The prey species themselves appeared adept at avoiding baboons with very few observations of the study group encountering small antelope species or individuals. In addition, few observations of aggressive defence by adult antelopes with young suggest they may be good at 'parking' young in safe locations. Taken together, these factors suggest baboons form an important component of smaller antelope species' 'landscape of fear' (Laundré et al., 2001) (i.e., spatial variation in perceived predation risk) as has been shown with the vervets at Lajuma (Willems and Hill, 2009). This may also be the case for other rarely encountered species such as mongoose, bushbabies, dassie, guinea fowl, francolin (and other birds), leporids, and rodents. Future research should explore the role baboons have in determining the space-use of other species. It may also be interesting to explore whether larger bodied antelope species such as bushbuck and klipspringer adapt their space-use during key reproductive periods (Crawford et al., 2019) to avoid neonatal predation by baboons.

### ANTELOPE PREDATION SEASONALITY

The rate of predations on young antelopes should reflect the abundance of young available at any given time; thus, we would anticipate antelope predation to be higher during calving seasons, particularly if fecundity is high. During the study we also experienced several periods of drought which likely influenced the stamina and mobility of fawns and the likelihood of them being 'parked' by their mothers, both of which likely increase the probability of predations by baboons. In 2017 the study area experienced a lengthy dry spell after a wet season with high rainfall. This may have contributed to greater antelope fecundity and so greater predation opportunities for the baboons as the dry spell wore on, as during the dry spell we observed up to 6 (two observations very likely but not confirmed) predations on young antelope across a 3-day period. Multiple antelope predations occurring within 4-day periods (one observation week) was also relatively common (n = 8) and may reflect similar seasonal dynamics.

Bushbuck have been observed to breed throughout the year (Fairall, 1968) although calving tends to peak at the onset of rainy seasons (Apio et al., 2009) with two peaks from March-June and August-November (Anderson, 1979), similar to duiker (Bowman and Plowman, 2002). Bushbuck predations occurred mostly during late rainy season and into the early stages of the dry season (March-May), although successful and unsuccessful attempts were made on young bushbuck throughout the year. However, calving seasonality may only skew predation rates on bushbuck and other larger antelopes at our site, as attempts on red duiker occurred throughout the year, and adult red duiker were preyed upon. As red duiker were rarely observed in proximity to baboons it is likely that all but the largest-bodied red duiker are at risk of baboon predation year-round.

### CAPTURE METHODS

Despite vertebrate tissue offering a high energy, high protein food source with a diverse range of micronutrients that aid numerous physiological processes (Watts, 2020), baboons are not thought to actively hunt (although see Strum, 1975). Our observations suggest this is generally the case in the Soutpansberg too with the baboon behaviours matching descriptions of opportunistic or scavenge hunters, as prey are typically encountered whilst the baboons are engaged in other behaviours (e.g., foraging for other resources) (Hamilton III and Busse, 1982; Sommer et al., 2016). The baboons did not appear to use a targeted bite or systematic strategy for killing prey and often pinned down/restrained live prey whilst beginning consumptions, similar to observations from elsewhere (Sommer et al., 2016).

Despite observing a lengthy prey chase, which suggested the baboons can rely on their superior stamina over the young antelope, chasing was rarely observed. Sommer et al. (2016) consolidated numerous observations of baboon predatory behaviour and reported that approximately 40% of prey animals were chased across all baboon species, whilst 60% seemed to be quickly grabbed after chance encounters, e.g., ‘parked’ fawns/neonates (Allsopp, 1978). It may be that the dense vegetation and rocky landscape at our study site made chasing challenging, although the same factors may have also been responsible for missed observations.

Our study group responded rapidly to visual and audible cues of several species (e.g., birds calls and flight, distress calls of young antelopes), suggesting they associate certain stimuli with predation opportunities. The group were regularly observed wafting long grasses/leaf litter, rolling rocks whilst foraging, and scanning tree canopies, likely searching for fruits, seeds, or invertebrates; however, such behaviours increase the likelihood of detecting small prey items such as lizards, rodents, or eggs/nestlings. If baboons utilise specific strategies to hunt prey, it is unlikely observers would be able to detect them pre-emptively, so it remains unclear whether or not the baboons exhibit any active hunting strategies. We also frequently observed baboons looking into rock crevices, which was performed by several individuals when attempting to predate a rock dassie. Thus, although these baboons clearly utilise opportunistic encounters with prey, there is the possibility they actively search for other opportunities as well. This may especially be the case during periods where encounter rates with suitable prey are high, e.g., calving seasons.

### WITHIN-GROUP FACTORS

It is likely we missed several capture events by female and juvenile classes as they often had blood on them when we arrived late to events with males already monopolising carcasses, although this could also be from unobserved scramble events. There does not appear to be any strong evidence to suggest certain age-sex classes play a more prominent role in predatory behaviours, therefore, as we observed numerous episodes of juveniles attempting to predate a range of species, including lizards, francolin, guinea fowl, antelope, rodents, dassies, and scrub hare. Given that this group seemed adept at quickly locating and gathering around kills (i.e., vulture response), and we observed multiple juveniles attempt to predate young/smaller antelopes of similar body sizes to themselves, it is interesting that the males had not developed strategies for predating large-bodied prey. However, it is likely the risks do not outweigh the reward (e.g., collective defence or strikes from warthog tusks and antler horns could result in serious injuries) and that without active or tolerated sharing between males, there is little impetus for cooperative predation techniques to develop. Given that female chacma baboons may trade grooming for other commodities such as resource access (Barrett et al., 1999), male monopolisation patterns may have inhibited the sharing tendencies amongst other age-sex classes, ultimately blocking the kin and reciprocation pathways that could allow cooperative strategies to emerge (Sachs et al., 2004).

We observed numerous instances of non-monopolising individuals acquiring scraps, three of which matched descriptions of passive meat-sharing (Goffe and Fischer, 2016) or tolerated theft (Stevens and Gilby, 2004). Several of the remaining observations matched Goffe and Fischer's (2016) definitions for 'scavenging' (i.e., the acquisition of meat after it has been left behind (>2 m) by the possessor) and 'stealing' (i.e., food transfer occurs despite resistance from the possessor); the latter we refer to as scrounging here. Our observations of individuals quickly 'stealing' scraps whilst monopolisers were distracted may be best described as 'undetected theft' given the monopoliser did not notice the scrounge occur and so did not protest as with 'stealing' (Goffe and Fischer, 2016). Although these opportunistic stealing and scavenging behaviours are not sharing in the active sense (i.e., intentionally providing a food item to another individual), they are generally considered forms of 'sharing' as meat consumption is divided amongst at least two individuals (Stevens and Gilby, 2004), albeit not equally in our study.

Given that agonistic behaviours often occurred between co-feeding individuals during scramble events, active meat-sharing (i.e., facilitated transfer) seems a poor fit for describing our observations. Alternatively, it could be argued that the initial predator was tolerating co-feeding from conspecifics, indicative of passive-meat sharing. Indeed Goffe and Fischer's (2016) definition of 'stealing' requires resistance from the 'owner' of the carcass, which may account for some of the agonism we observed. However, given there was no sole 'possessor' of the carcass once multiple individuals had joined, we feel these scramble episodes represent 'contested' sharing instead. This distinction is important when considering the benefits of food-sharing. As many individuals achieved minimal food shares and the lack of a clear 'owner' made reciprocation redundant, the negative consequences (i.e., injury or death) of competing for access to the meat was unlikely to be offset by the immediate (e.g., food intake) and delayed (e.g., reciprocation) benefits typically associated with food-sharing (Stevens and Gilby, 2004).

There were clear sex differences in terms of monopolisation, with males always monopolising antelope kills and also acquiring francolin, small birds, python eggs, and skinks after other individuals had made the kill/discoveries. Only two scrounging and monopolising events were observed for non-adult and adolescent male age-sex classes, with the dominant female scrounging a rodent and a juvenile male (dominant female's son) monopolising a scrounged francolin. It has been suggested previously that male baboons acquire more of their vital nutrients through vertebrate feeding whilst females do so via invertebrate feeding (Hausfater, 1976). However, in this group invertebrate foraging was frequently observed in all age-sex classes and vertebrate meat was readily consumed by all age-sex classes, including infants (consumed scraps twice). The sex differences in monopolisation tendencies therefore highlight that males were exploiting competitive asymmetries in order to monopolise carcasses, limiting opportunities for smaller and subordinate group members to consume highly desirable vertebrate meat.

Aggressions were related to rank instability amongst males, however, all antelope predation events seemed to elicit a broad 'vulture response' in the group (Altmann and Altmann, 1970; Sommer et al., 2016) with higher ranking individuals most often in proximity to monopolisers. Given monopolisers sometimes did not move much during consumption, public-information on meat-eating was available allowing individuals to learn socially (Danchin et al., 2004; Dall et al., 2005) and may be an important aspect in why all group members remain attentive to numerous visual and audible cues. Many of the males observed the dominant male (ID: DAV) access brain tissue consistently during his monopolisation episodes. Despite watching (and subsequently attempting) to access brain tissue themselves, only one other male was observed achieving this on a young fawn, despite all of them making attempts (although other males were observed achieving this pre-2014 – DAV was present during those observations however). Although it is unclear why others failed in this process during our study period, they were all observed attempting to bite as far into the corner of their mouths as possible, while the most successful male (ID: DAV) achieved it using his incisors. It is unclear whether the successful male simply had more powerful jaw muscles or his specific technique was the key; if it was the latter then it may suggest the other males were unable to learn this technique through trial and error or socially, despite observing it several times. Nevertheless, it suggests brain material was reluctantly discarded on several occasions, especially if individuals managed to successfully isolate themselves with the carcass.

With respect to information acquisition and learning, an event was observed in which a relatively high-ranking adult female (ID: SIL) uncovered a bushbuck fawn parked and concealed in long-grass. Upon discovery of the fawn, the female baboon immediately grabbed, pinned, and bit the fawn, but seemed to lack an effective technique for killing and consuming any part of the animal quickly, despite dominant females achieving this task relatively quickly. It could also be related to social fear, as the individual (ID: SIL) seemed nervous (glancing and flinching repeatedly), and was quickly charged by the dominant females as soon as the fawn's distress calls were heard, resulting in the fawn being scrounged before being killed. This was the only observation where this female (ID: SIL) was seen during the early stages of meat-eating, but it may suggest that unless subordinate members are able to subdue prey quickly, and so prevent distress calls, then the prey will likely be scrounged. Such processes may block personal information and learning how to improve predatory methods, leading to a scenario whereby dominant individuals achieve disproportionate success relative to subordinate animals.

### DISCARDING OF PREY ITEMS

Predation by wild primates on prey species has often been discussed from the perspective of the evolution of social traditions (e.g., Strum, 1975) and less work has discussed ways in which these behaviours may affect the wider ecosystem. For example, discarded animal matter can be an important contributing factor in supporting biodiversity (Wilson and Wolkovich, 2011; Moleón et al., 2015; Inger et al., 2016). Carrion eaters enhance the connectivity within food webs and the transfer of energy between different trophic levels, thus enhancing ecosystem stability. As a result, any animal that contributes to the process of carrion provision is potentially providing an important role in the ecosystem.

One of the baboon's key behaviours whilst feeding on meat was to flee to block public information about prey items (i.e., information withholding or secrecy; Derex et al., 2014), therefore minimising the likelihood of competition. This process also limits the likelihood of subordinate baboons feeding on remains, allowing scavenger species greater opportunities (Moleón et al., 2015). Even minor scraps being discarded has the potential to attract animals (e.g., genets, civets, honey badger, birds), and could be important resources increasing microbial biomass in soils and support a variety of carrion reliant arthropod and fungi communities (Barton et al., 2013).

## CONCLUSIONS AND FUTURE DIRECTIONS

We provide a detailed multi-year study of the vertebrate predatory and meat-eating behaviours of baboons occupying the Soutpansberg Mountains, South Africa. As with baboon groups elsewhere (Sommer et al., 2016), predations appear mostly opportunistic, although we cannot rule out routine searching for vertebrate prey, such as looking into crevices for dassies or searching tree canopies for birds' nests. Adult and adolescent males monopolise most prey items, similar to findings elsewhere (Sommer et al., 2016); however, individuals were adept at finding isolated locations beyond the periphery of the group that limited public knowledge of the prey items. We observed several scramble kleptoparasitism episodes which do not appear to have been reported in meat-eating contexts before in baboons, although mobbing of predators is commonplace. Despite predation and meat-eating episodes being common on bushbuck and red duiker at Lajuma, bushbuck have only been observed as prey in two other studies and duiker once (see Sommer et al., 2016).

Although discarded items from baboons are unlikely to be a major source of carrion compared with carnivores that take much larger prey, it represents just one of many roles the baboons may play in their native ecosystems. In semi-arid Karoo ecosystems baboons are known to be key seed dispersers of numerous plants species (Tew et al., 2018) and one of the only animals to dig and move rocks (Maré et al., 2019). In both cases baboons were considered keystone species for their roles as endozoochores and zoogeomorphic agents. At our field site the baboons also consume and disperse seeds of various endemic plants, dig and move rocks routinely and influence prey species space use (vervets, see Willems and Hill, 2009), whilst also preying on a range of invertebrate and vertebrate species. Given that unhabituated groups of baboons were also observed preying on vertebrate species in the study area, as were the habituated group when not being observed by researchers, the overall contribution of baboons as a mesopredators in the Soutpansberg Mountains ecosystems may be currently underappreciated.

The baboon's success in calving seasons could have an important impact on antelope (particularly bushbuck) population growth, particularly if this is on top of the impact of fear (Creel and Christianson, 2008), and this may have implications for larger predators like leopards and brown hyaena who predate bushbuck frequently at Lajuma (Williams et al., 2018). As the local leopard population is declining (Williams et al., 2017) baboons could predate on young antelope more frequently, a common response of mesopredators when apex predators are in decline (Ritchie and Johnson, 2009). The study group have also acted aggressively towards leopards (one observation of mobbing), honey badgers, and crowned eagles (see table 1), and previously killed a rock python who attempted to predate a juvenile baboon (Peter Tomlin, pers. comm.). As such, their ecological role in the Soutpansberg may have been undervalued and should be explored in more detail in the future. This is especially important as baboon groups are known to be persecuted in the region for their perceived negative impacts on farming and livelihoods, but this could significantly undervalue their importance to local ecosystems.

Despite inhabiting a dense and complex habitat mosaic which is generally thought to hinder baboon predations, this study group has a higher predation rate than typically observed in chacma and baboon populations generally, with various species predated across a range of habitats in the study area. However, future research needs to explore ways of collecting detailed data on these processes in primates, as opportunistic data has thus far been unable to reliably ascertain precise species-specific predation rates. The red colobus-chimpanzee system is an obvious exception to this (Boesch, 1994; Mitani and Watts, 1999; Teelen, 2008; Watts and Amsler, 2013; Bugir et al., 2021), yet it remains unclear how habituation influences predation rates in this scenario (LaBarge et al., 2020b) (see supplementary text S1 for discussion). Future research should investigate primate predatory and meat-eating behaviours explicitly, instead of relying on opportunistic observations during other data collection protocols but pay careful attention to the role the observers may play in any predator-prey dynamics.

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## Statement of ethics

All research methods included in this study were performed in accordance with the relevant guidelines and regulations, under ZA/LP/81996 research permit, with ethical approval from the Animal Welfare Ethical Review Board (AWERB) at Durham University. The authors confirm the study was carried out in compliance with ARRIVE guidelines.

## Conflict of interest statement

We declare no conflicting interests.

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## Author contributions

AA conceived the study. RH and CH conceived the original methodology. AA, LRL, ALB, BJ, ZM, TP, FS, AW, AFW, and HW assisted with the evolution of the study and formulating the final goals and aims of the project. AA, LRL, CH, ALB, BJ, ZM, TP, FS, AW, AFW, and HW collected data on predation events and inter-species encounters. AA and LRL drafted the initial manuscript. CH, ALB, BJ, ZM, TP, FS, AW, AFW, HW, and RH critically revised the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

## Data availability

All data is provided in the main text.

## Supplementary material

Supplementary material is available online at: https://doi.org/10.6084/m9.figshare.20457027

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