

RESEARCH ARTICLE

Meat eating in wild hamadryas baboons: Opportunistic trade-offs between insects and vertebrates

Amy L. Schreier^{1,2,3}  | Renate M. Schlaht¹ | Larissa Swedell^{2,3,4,5} ¹Department of Biology, Regis University, Denver, Colorado²Department of Anthropology, The Graduate Center, City University of New York, New York, New York³New York Consortium in Evolutionary Primatology, New York, New York⁴Department of Anthropology, Queens College, City University of New York, New York, New York⁵Department of Archaeology, University of Cape Town, Cape Town, South Africa**Correspondence**

Amy L. Schreier, Department of Biology, Regis University, 3333 Regis Blvd. D-8, Denver, CO. Email: aschreier@regis.edu

Funding information

City University of New York PSC-CUNY Research Award Program, Grant/Award Number: Award #66588-0035; New York Consortium in Evolutionary Primatology; City University of New York PhD Program in Anthropology

Abstract

The consumption of meat may provide herbivorous animals with important nutrients that are scarce in their plant-based diet. Seasonal variation in plant food availability has been suggested to motivate dietary flexibility in a range of species and thus primates may seek more prey when key plant resources are unavailable. Alternatively, prey encounter rate may drive meat eating. Here we investigate patterns of meat eating in hamadryas baboons (*Papio hamadryas*) at Filoha, Awash National Park, Ethiopia. The Filoha baboons rely largely on doum palm fruit (*Hyphaena thebaica*), which are available most months of the year, and the young leaves of *Acacia senegal*, which are more abundant during the wet season. We hypothesized that the baboons would consume more meat when *H. thebaica* and *A. senegal* were less available, which we tested by comparing meat eating and consumption of these plant food species from March 2005 through February 2006. Our results reveal a high rate of vertebrate meat eating at Filoha (0.028/hour of observation) compared with other hamadryas sites. We found no relationship, however, between meat eating (either insect or vertebrate) and either rainfall or consumption of *H. thebaica* or *A. senegal*, indicating that availability of preferred plant resources does not drive meat consumption. Vertebrate consumption and time spent feeding were significantly negatively associated; there was no relationship, however, between the consumption of animal matter and either home range size or daily path length. Vertebrate and insect consumption alternated throughout the year such that the baboons maintained a small amount of animal matter in their diet year-round. Our results suggest that the baboons do not often actively seek animal matter, but consume it opportunistically, with the presence of locust and dragonfly swarms driving insect consumption, and both prey availability and the availability of feeding time shaping vertebrate predation.

KEYWORDS

doum palm, insect consumption, insect swarms, time budgets, vertebrate predation

1 | INTRODUCTION

An increasing body of research has documented meat eating in species that were previously thought to rely solely on plant

resources. Both smaller frugivorous primates and large herbivores such as gorillas (*Gorilla gorilla*, *Gorilla beringei*) eat insects to supplement a diet of fruit and leaves (Rothman, Raubenheimer, Bryer, Takahashi, Gilbert, 2014; Cords, 1986; Deblauwe, 2009;

Ganas & Robbins, 2004). L'hoest's monkeys (*Cercopithecus lhoesti*) and blue monkeys (*Cercopithecus mitis*) in Uganda, for example, spend at least half of their feeding time-consuming invertebrates (Tashiro, 2006), and at Dja Biosphere Reserve in Cameroon 11% of gorilla feeding samples consist of insects (Deblauwe and Janssens, 2008).

Other primates – including baboons (*Papio hamadryas*, *Papio anubis*; Rhine, 1986, Swedell, 2006), capuchin monkeys (*Cebus capucinus*; Rose et al., 2003), and orangutans (*Pongo abelii*; Buckley, Dench, Morrogh-Bernard, Bustani, & Chivers, 2015) – are known to consume larger vertebrates ranging from squirrels and hares to dik diks and antelopes. Perhaps the best known example of meat-eating among primates is the chimpanzee, which hunts in groups and consumes other primates, such as redtail and red colobus monkeys (Boesch & Boesch, 1989; Gilby & Wrangham, 2007; Gilby, Eberly, Pintea, & Pusey, 2006; Mitani & Watts, 2001, 2005; Stanford, 1994, 1998, 2008; Tennie, O'Malley, & Gilby, 2014; Watts & Mitani, 2002). Chimpanzees capture and consume red colobus monkeys so frequently that it has led to the decline of colobus populations in some areas (Watts & Amsler, 2013; Watts & Mitani, 2002).

With the exception of tarsiers, which are faunivorous, the reason for meat consumption in most primates remains unclear. Most hypotheses relate to nutrition, with the micronutrient hypothesis, for example, suggesting that because animal products contain many unique micronutrients, the consumption of meat is a means to supplement the diet with micronutrients that are not found, or are scarce or inaccessible, in plant foods (Hamilton & Busse, 1978; Tennie et al., 2014). In particular, meat is high in vitamin B-12 (Lambert, 2011; Williamson, Foster, Stanner, & Buttriss, 2005), whereas vegetation lacks this vitamin (Lambert, 2011). Meat is also high in zinc and iron (Milton, 2003; Tennie et al., 2014). In addition to important vitamins and minerals, animal matter may also provide omnivorous primates with a source of high-quality protein (Chapman, Rothman, & Lambert, 2012), including all essential amino acids. Although plants supply most of the protein in primate diets, animal protein has greater nutritional value due to its more favorable ratio of amino acids (Hamilton & Busse, 1978; Williamson et al., 2005). Alternatively, primates may consume animal matter simply for its high caloric value (Hamilton & Busse, 1978). By consuming meat opportunistically, omnivorous primates may gain greater net energy per unit time for each successful kill than by foraging on only plant matter.

Meat eating in noncarnivorous animals also appears to relate to dietary flexibility, which may be favored in habitats with wide seasonal variation in food availability. The nutrient shortfall hypothesis suggests that seasonal resource scarcity often forces a shift in the diet to consume sufficient nutrients for survival (Gilby et al., 2006; Mitani & Watts, 2001; Teleki, 1973). This may be the result of a specific nutrient deficiency or of a general lack of nutrients in the diet (Mitani and Watts, 2001). In white-faced capuchins (*C. capucinus*) at Santa Rosa National Park, Costa Rica, for example, Rose (1997) found clear seasonal variation in meat eating, with the capuchins both consuming more meat and engaging in more successful predation attempts in the dry season compared with the wet season.

Hausfater (1976) hypothesized that, in baboons, temporal fluctuation in arthropod availability leads to a fluctuation in dietary B-12 that might motivate increased predation at certain times of the year.

Baboons are known to consume meat on an occasional and opportunistic basis nearly everywhere they occur (Davidge, 1978; Davies & Cowlshaw, 1996; Goffe & Fischer, 2016; Rhine, 1986; Strum, 1975, 1983; Whiten, Byrne, & Henzi, 1987; Whiten, Byrne, Barton, Waterman, & Henzi, 1991). Yellow baboons (*P. cynocephalus*), for example, prey on vertebrates such as lizards (*Varanus spp.*), birds, hares (*Lepus*), and gazelle (*Nanger granti*) at Amboseli National Park, Kenya (Altmann & Altmann, 1970; Hausfater, 1976) and Mikumi National Park, Tanzania (Rhine, 1986). The baboons at Amboseli also eat locusts (Altmann & Altmann, 1970), whereas those at Mikumi spend, on average, almost 20% of their monthly feeding time consuming insects (Rhine et al., 1986). Guinea baboons in Niokolo-Koba National Park, Senegal hunt young antelope, hares, and birds (Goffe & Fischer, 2016), and olive baboons (*P. anubis*) at Gilgil, Kenya prey on Thomson's gazelle (*Eudorcas thomsoni*), Cape hares (*Lepus capensis*), and dik dik (*Madoqua kirki*) (Strum, 1975). The Pump-house troop developed a systematic method of predation, which included hunting and rudimentary meat sharing. By presenting baboons with gazelle carcasses and live domestic rabbits, Strum (1983) found that the physical and historical context of the prey – for example, how recently it was killed and by which individual – was a major factor driving individual feeding behavior, and that overall the baboons hunted opportunistically but avoided scavenging. Davies and Cowlshaw (1996) observed chacma baboons (*P. ursinus*) in the Namib Desert, Namibia preying on an antelope calf (*Oreotragus oreotragus*) followed by competition between the baboons and black kites (*Milvus migrans*) over the prey. The authors concluded that, whereas this particular predation event was opportunistic, chacma baboons do occasionally search actively for both invertebrate and vertebrate prey (Davies & Cowlshaw, 1996). Chacma baboons in South Africa eat grasshoppers (Orthoptera), shellfish (*Patella granularis*), and shark eggs in the Cape of Good Hope Nature Reserve (Davidge, 1978; Lewis & O, Riain, 2017; Lewis, West & O, Riain, 2018) and those in the Giant's Castle Reserve in the Drakensburg Mountains feed on invertebrates (Whiten et al., 1987; Whiten et al., 1991).

Observations of meat eating by hamadryas baboons (*P. hamadryas*) have so far been limited compared to other baboons. In a broad sample of several hamadryas groups near Erer Gota, Ethiopia, Kummer (1968) observed no direct instances of vertebrate predation during a 1-year period, only one presumed meat-eating event in which a 3-year-old female baboon carried a dead dik dik (*Madoqua kirki*), which he later found as a partially eaten fresh carcass. The troop also fed on locusts when a swarm settled near their sleeping site. Abegglen (1984) did not report seeing any direct cases of predation or meat-eating among the Cone Rock Troop of hamadryas at Erer Gota, having witnessed only a single occurrence over a year and a half in which a subadult male carried a dead rock hyrax in its mouth but did not eat it. At the Filoha site in Awash National Park,

Ethiopia, Swedell (2006) observed three instances of hamadryas meat eating over 18 months, for one of which she also witnessed the predation event, all of which were Abyssinian hare (*Lepus capensis habessinicus*). The focus of all three of the above studies, however, was social behavior rather than feeding ecology, and observations were concentrated at or near sleeping sites rather than throughout daily foraging.

In this study, we examine predation and meat eating by wild hamadryas baboons at Filoha, Awash National Park, Ethiopia from March 2005 through February 2006. The Filoha region consists of *Acacia* scrublands, grasslands, and cliffs, all of which are typical of hamadryas habitat in other parts of their geographic range (Al-Safadi, 1994; Biquand, Biquand-Guyot, Boug, & Gautier, 1992; Kummer, 1968; Sigg & Stolba, 1981; Swedell, 2006; Zinner, Peláez, & Torkler, 2001). Unlike many other areas inhabited by hamadryas baboons, however, the Filoha area also includes hot springs, swamp vegetation, and palm forests, which provide a high concentration of doum palm fruit (*Hyphaene thebaica*), a preferred food resource (Schreier, 2010; Swedell, 2002, 2006; Swedell, Hailemeskel, & Schreier, 2008). Doum palm fruits and the leaves, flowers, seeds, and sap of *Acacia senegal* comprise the largest portions of the diet of Filoha baboons (Schreier, 2010; Swedell et al., 2008). The availability of doum palm fruit varies throughout the year, with the lowest in September and October (Schreier, 2010). This reduced availability of doum palm fruit places a constraint on group size, as hamadryas bands (larger social units) are more likely to split into clans (smaller social units) during this time (Schreier & Swedell, 2012).

Although nutritional analyses of plant species at Filoha have not yet been conducted, Aboshora et al. (2014) examined the nutritional properties of doum palm fruit collected from a garden in Sudan. Their results suggest that doum palm fruit is a good source of essential minerals, including calcium, magnesium, sodium, and potassium, and is also rich in B-complex vitamins (Aboshora et al., 2014). Nutritional analyses of two closely related species, *H. coriacea* and *H. compressa*, also indicate that palm fruit is rich in a variety of important minerals, including iron and zinc (Hoebekke, 1989; Lokuruka, 2007), both of which are also found at high levels in insects (Deblauwe & Jannsens, 2008). Nutritional analyses of other palm species suggest high lipid content, especially in the pulp, the part of the plant that the baboons consume; fatty acids are substantially higher in pulp oils than kernel oils in *Syagrus olearacea*, *Syagrus romanzoffiana*, and *Acromonia aculeata* (Cardoso Coimbra & Jorge, 2011). Energy content (kcal) of doum palm fruit appears to be equivalent to other plant resources (Aboshora et al., 2014), although its clumped distribution and high abundance during certain times of the year likely provides the baboons with more concentrated energy than more dispersed resources. Doum palm fruit is not especially high in protein, however, and Filoha baboons likely obtain most of their protein from the leaves of *Acacia* and *Grewia* shrubs (Schreier, 2010; Swedell et al., 2008). Young leaves have higher protein content than mature leaves (Lambert, 2011), and hamadryas at Filoha appear to particularly prefer the young leaves of *A. senegal*, which are available at Filoha during and just after the wet season, in July, August, and September (Schreier, 2010).

Here we seek to assess the influence of environmental conditions and preferred food availability on predation and meat eating by hamadryas baboons. We hypothesize that seasonality in availability and consumption of preferred plant food resources shapes temporal patterns of procuring and eating animal matter, which we predict the baboons would spend more time doing when preferred plant resources are less abundant. Namely, we predict that:

1. Hamadryas baboon meat eating at Filoha will be negatively associated with rainfall as fresh leaves are more abundant in the wet season compared with the dry season (Schreier, 2010).
2. Hamadryas baboon meat eating at Filoha will be negatively related to the contribution of doum palm fruit and *A. senegal* leaves to the diet.

Alternatively, if Filoha baboons eat meat on a purely opportunistic basis, minimizing time and energy costs by capturing prey at close range without a search or chase (Hamilton & Busse, 1978), then meat eating should increase with additional encounters with prey. If so, we predict that:

1. Meat eating will be positively related to home range size and daily path length because further travel will increase encounters with animal prey.
2. Meat eating will be positively related to time spent traveling (as more travel will increase potential prey encounters) and negatively associated with time spent feeding (as less time spent feeding on plant resources will free up time to pursue animal prey).
3. The baboons will eat more meat during times when they forage as separate clans instead of a cohesive band, as prey are less likely to flee from smaller numbers of baboons and this would increase individual prey encounter rate.

2 | METHODS

2.1 | Study site & study subjects

This study took place at the Filoha outpost of Awash National Park in central Ethiopia from 5 March 2005 through 11 February 2006, when we followed and observed a band of approximately 200 hamadryas baboons ("Band 1", previously called "Group 1": Schreier & Swedell, 2008, 2009, 2012; Swedell, 2002, 2006; Swedell & Tesfaye, 2003; Swedell et al., 2008) for 1342 hr. Band 1 comprised a total of 32 one-male units (OMUs) over the course of the study period, each consisting of a leader male, one–nine adult females, and juveniles, and infants (Schreier & Swedell, 2008, 2012). The outpost is surrounded by about 2 km² of natural hot springs, doum palm trees, swamp vegetation, and a 1.5 km-long cliff serving as one of the study band's multiple sleeping sites (Swedell, 2002, 2006; Figure 1). The surrounding area consists of *Acacia* scrublands and open grasslands typical of other hamadryas habitats. The Filoha region is

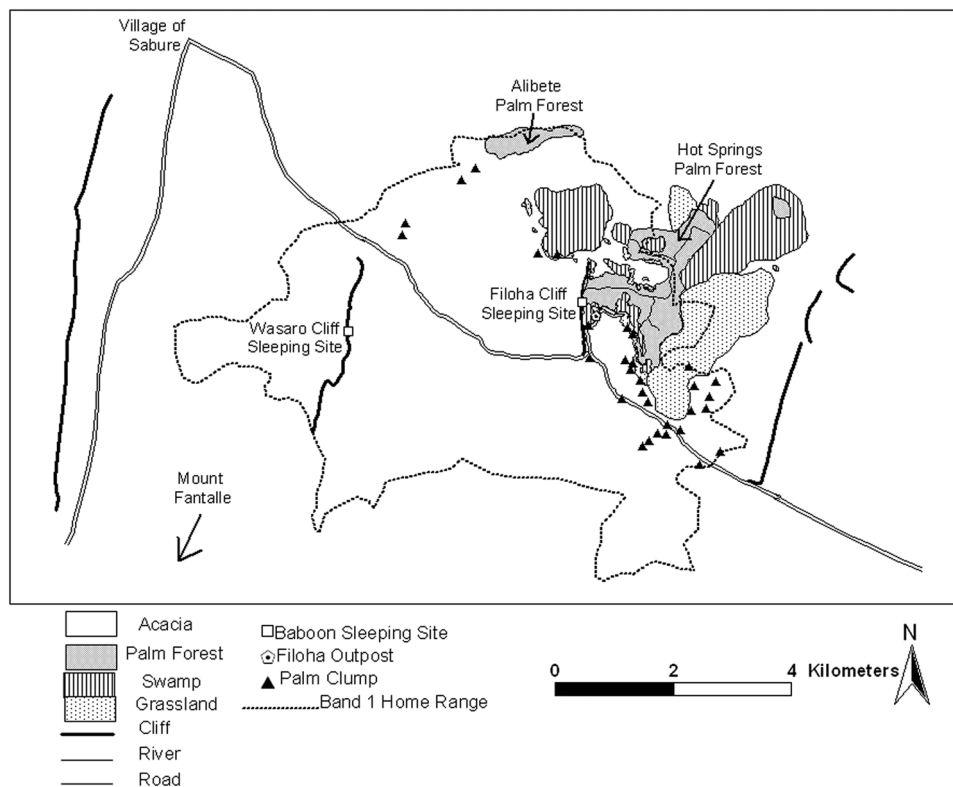


FIGURE 1 Map of the Filoha region

characterized by year-round high temperatures, with an average daily temperature of 31.5 degrees Celsius during the study period (Schreier and Swedell, 2009). The Awash region receives two periods of rainfall each year—frequent, concentrated rainfall between June and September (the long rains), and more sporadic rainfall between February and May (the short rains; Swedell, 2006). During the study period, total rainfall was 606.7 mm, almost half of which occurred in July and August (Schreier and Swedell, 2009). Between June 30 and August 31, 2005, 324 mm of rain fell at Filoha; between October 2005 and February 2006, by contrast, rainfall totaled just 26.5 mm.

In addition to hamadryas baboons, Filoha is home to many potential prey and predator species. Other fauna include warthog (*Phacochoerus aethiopicus*), lesser kudu (*Strepsiceros imberbis*), Defassa waterbuck (*Kobus ellipsiprymnus defassa*), dik dik (*Madoqua saltiana*), Abyssinian hare (*Lepus capensis habessinicus*), black backed jackal (*Canis mesomelas*), rock hyrax (*Procapra habessinica*), bat-eared fox (*Otocyon megalotis canescens*), porcupine (*Hystrix cristata*), caracal (*Caracal caracal nubica*), leopard tortoise (*Testudo pardalis*), guinea fowl (*Numida meleagris*), francolin (*Francolinus spp.*), and crocodile (*Crocodylus niloticus*) (Schreier and Swedell, 2009). Potential predators such as lion (*Panthera leo*), spotted hyena (*Crocuta crocuta*), leopard (*Panthera pardus*), and various snake species also inhabit the Filoha region (Schreier and Swedell, 2009).

Permission to conduct research at Filoha was granted by the Ethiopian Wildlife Conservation Authority, and the research adhered to the legal requirements of Ethiopia. Protocols were approved by the Queens College Institutional Animal Care and Use Committee

and adhered to the American Society of Primatologists principles for the ethical treatment of primates.

2.2 | Data collection and analyses

2.2.1 | Home range size and daily path lengths

To quantify home range size and daily path lengths (DPL), during all-day follows we mapped the geographic center of the band every 15 min (e.g., Sigg & Stolba, 1981) using a Garmin etrex Legend handheld Global Positioning System (GPS) unit. We defined home range as the total area used by the band over the course of a specified period (e.g., entire study period, month) and calculated it as the minimum convex polygon, which includes all recorded locations (from full and partial observation days), using ArcView GIS 3.1 software (ESRI, 2001, Redlands, CA; Ostro, Young, Silver, & Koontz, 1999). DPL was determined based on observation days for which we recorded complete daily travel routes (i.e., from the morning to evening sleeping-site locations; e.g., Altmann & Altmann, 1970; Sigg & Stolba, 1981). We computed DPL by summing the distance between all mapped locations. We calculated mean DPL for the entire study period as well as for each month. In September the baboons spent more time farther south, closer to Mount Fantalle (about 15 km southwest of Filoha), as they often do during the long rains, and thus we could not record complete travel routes; we, therefore, could not calculate mean home range size or DPL for this month.

2.2.2 | Activity patterns and preferred plant species and insect consumption

During all-day follows of the study band, we conducted 30-min focal samples of focal OMUs during which we conducted instantaneous scan samples at 2-min intervals (Altmann, 1974). At each interval, we recorded the activity (i.e., rest, social, feed, travel) of the leader male and each adult female in the OMU. When individuals were feeding, we recorded the food item at the species level and the plant part being eaten. When individuals fed on insects, we recorded the type of insect when identification was possible. We aimed to collect equal amounts of data for each OMU; analyses are based on the 31 OMUs for which we have at least 50 instantaneous scan samples. We calculated the contributions of different food species to Band 1's annual feeding habits as a proportion of the total number of all feeding records. Monthly feeding habits were calculated as proportions of the feeding records for each month. We calculated time spent feeding and traveling as a proportion of the total activity records. Initial analyses showed no differences in activity patterns or the consumption of plants or insects between sexes thus we include both males and females in the analyses presented here.

2.2.3 | Vertebrate consumption

Data on vertebrate meat eating were collected on an *ad libitum* basis. For instances in which vertebrate meat eating was observed but the predation event was not, we assumed that the prey was captured and killed by the baboon itself rather than scavenged due to the lack of any observations at Filoha, either during this study period or others (e.g., Swedell, 2002; 2006), of baboons eating carcasses left by other predators. Each successful predation event that was observed was counted as one instance of meat eating; each vertebrate meat-eating event (when predation was not observed) was also counted as a single instance. Each individual prey animal was counted as a single meat-eating event, even if there were multiple baboons eating from the same carcass. We recorded the age-sex class of all individuals observed feeding on a carcass. We calculated the hourly rate of vertebrate meat-eating for each month of the study period by dividing the number of meat-eating instances by the total number of hours of baboon observations for that month. Data on unsuccessful predation attempts (that did not result in the capture of the prey item) were not included in the calculations of predation and meat-eating rates; these observations were *ad libitum* as we did not systematically record attempted predation. To examine the effect of group size on meat eating we compared vertebrate meat eating rate between the periods when Band 1 functioned as two approximately equal-sized independent clans (which occurred for at least 37 days over the study period) to when it remained as a cohesive band. We also compared contribution of insects to the diet during these two periods.

2.2.4 | Associations between meat eating and seasonality, ranging, and activity patterns

We conducted Spearman rank correlation analyses to test for relationships between meat eating and (a) rainfall, (b) consumption

of palm fruit and *A. senegal*, (c) home range size and DPL, and (d) time spent feeding and traveling. To do so we compared the monthly hourly rate of vertebrate meat eating and a monthly contribution of insects to the diet with monthly rainfall, the contribution of palm fruit and *A. senegal* leaves to the monthly diet, mean monthly DPL and home range size, and proportion of time spent feeding and traveling each month. We used SPSS version 23 for all analyses and significance was set at $p < 0.05$.

3 | RESULTS

We observed Band 1 for a total of 1342 hr across 159 days between 5 March 2005 and 11 February 2006 (Table 1).

3.1 | Home range size and daily path lengths

Band 1's home range was at least 38.6 km². Mean monthly home range was 12.8 km², with the largest home range sizes in June and July at 22.1 km² and 19.1 km², respectively. Conversely, the baboons ranged over the smallest areas in August (5.0 km²) and October (4.8 km²). Band 1's mean DPL was 8.3 km (± 2.04 , $N = 105$; range = 4.6–14.2 km). The baboons traveled the shortest distances in October (6.0 km), whereas their daily paths were longest in July (11.0 km).

3.2 | Activity patterns

We collected 12,969 activity records during focal samples of OMUs. Over the course of the study period, the baboons spent 29.0% of the time feeding and 27.6% percent of the time traveling. Activity patterns varied across months; the baboons spent the least amount of time feeding (26.0%) in June and fed the most in August (32.9%). Furthermore, the baboons spent the least amount of time traveling (22.8%) in October and traveled the most in July (30.8%).

3.3 | Plant consumption

We collected 3,761 feeding records during focal samples of OMUs. The baboons fed most frequently on the seeds, leaves, and flowers of *Acacia senegal* (23.0%), followed by doum palm fruit (*Hyphaene thebaica*; 20.4%). No other food species made up more than 9.5% of the baboons' annual diet. *A. senegal* contributed at least 11% to the feeding records each month, and more than 20% in 8 months (Table 1). *H. thebaica* made up at least 20% of the feeding records during 7 months and was the most frequently eaten species during six of them. It did not, however, contribute more than 8% of the feeding records in the remaining 5 months, and the baboons were not observed eating any doum palm fruit during August or September.

TABLE 1 Monthly observations, ranging patterns, and *Hyphaene thebaica* and *Acacia senegal* consumption of Filoha hamadryas baboons

Month	Hours of Observation	Days of Observation	<i>Hyphaene thebaica</i> contribution to diet (%)	<i>Acacia senegal</i> contribution to diet (%)	Monthly home range size (km ²)	Mean daily path length (km)
March 05	129.0	19	36.3	18.7	10.5	9.7
April 05	185.0	19	25.1	20.2	15.0	8.7
May 05	140.0	15	25.2	23.5	11.6	9.3
June 05	129.5	13	19.7	40.3	22.1	9.3
July 05	73.8	10	8.2	24.8	19.1	11.0
August 05	78.5	10	0	20.9	5.0	7.3
September 05	24.3	4	0	11.1	**	**
October 05	153.3	18	4.9	24.1	4.8	6.0
November 05	85.7	11	4.2	24.7	15.8	7.5
December 05	167.2	17	32.8	17.0	12.9	6.4
January 06	107.1	13	32.1	15.9	11.5	8.5
February 06	68.6	10	31.5	32.4	12.7	7.1
Annual	1342.0	159	20.4	23.0	38.6	8.3

**No complete travel routes (i.e., morning sleeping site to evening sleeping site) during September and thus DPL and home range size could not be calculated.

3.4 | Insect consumption

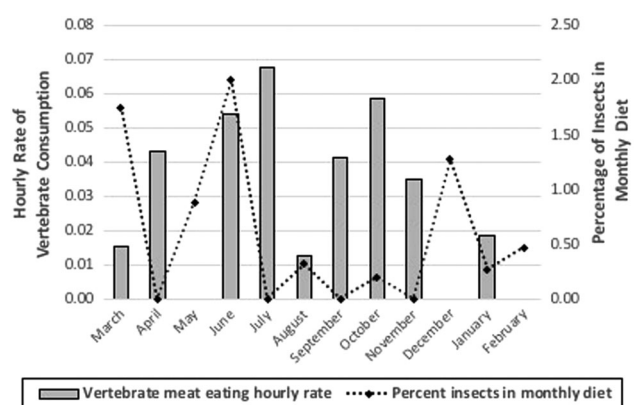
Insects made up 0.5% of the baboons' annual diet, ranging from 0% to 2% of monthly diets (Figure 2). The baboons' insect consumption consisted primarily of locusts (Orthoptera) and dragonflies (Order Odonata). Most of this feeding occurred when swarms of these organisms passed through the Filoha region. In almost all of these cases, most members of the band simultaneously fed on these insects, chasing and jumping up to capture and eat them. Predation success was high with the baboons catching an insect during the majority of attempts; the very large numbers of these insects during outbreaks allowed the baboons to repeatedly catch insects over a period of time generally lasting from 30 min to 1 hr. Almost all insect eating occurred in *Acacia* scrubland habitat where they spent almost half of their time, although the baboons fed on dragonflies a few times when a swarm passed through their sleeping cliff.

3.5 | Vertebrate consumption

Over the course of the study period, we observed the Filoha baboons eating vertebrate meat 38 times, at a rate of 0.028/hr of observation (CI: 0.020–0.038). Meat eating varied temporally, with a peak in April (8 instances; 0.043/hr) and an absence of vertebrate meat eating in May, December, and February (Figure 2). We observed the baboons killing prey 11 of these 38 times. On the occasions in which direct predation was not observed, the baboons were found eating freshly killed animals; while we cannot be certain that these were all the result of predation, none of these instances were clearly scavenging. Of the 38 meat-eating instances, 12 were dik dik, 7 were Abyssinian hare, 7 were Guinea fowl, 3 were lesser kudu, 3 were unknown birds, 3 were lizards (*Latastia longicaudata*), 1 was a francolin, and 1 was a rock hyrax. In one instance, the consumed meat was unidentifiable.

The majority of vertebrate meat eating occurred in *Acacia* scrubland habitat (where the baboons spent almost half of their time), with just four instances occurring in open grasslands (6% of their time), and twice the baboons ate vertebrate meat at their sleeping cliff where they spent about a quarter of their time. We did not observe the baboons consume vertebrate meat in palm forests, despite the fact that they spent 16% of their time in this habitat type over the course of the study period.

A total of 63 baboons were observed feeding on these 38 carcasses: 40 adult males, 14 adult females, and nine juveniles. Twice, females and their leader males consumed meat together; in each case, the female sat within 1 meter of the male and ate portions of the carcass without receiving any threats or aggression from the male. In all other cases, the meat was eaten by only one individual at a time. During the other occasions in which more than one baboon fed from the same carcass, the meat was scavenged, that is, other baboons ate animal remains only after the original baboon traveled

**FIGURE 2** Temporal patterns of consumption of vertebrate meat eating and insect eating

away, maintaining a distance of several meters but not approaching or attempting to eat any meat until the original baboon departed. In several cases, other baboons (both males and females from different age classes) often sat nearby, sometimes in contact with the meat eater, but did not attempt to eat any meat.

3.6 | Associations between meat eating and seasonality, ranging, activity, and group size

Contrary to predictions, there was no clear association between meat eating and seasonality. The relationship between the hourly rate of vertebrate meat eating and monthly rainfall was positive but nonsignificant ($r_s = 0.360$, $p = .251$, $N = 12$), and the relationship between insect eating and rainfall was negative but nonsignificant ($r_s = -0.495$, $p = .102$, $N = 12$). There was a moderate but nonsignificant negative relationship between hourly rate of vertebrate meat eating and contribution of palm fruit to monthly diet ($r_s = -0.496$, $p = .101$, $N = 12$) and no relationship between either vertebrate or insect consumption and the contribution of *A. senegal* leaves to the baboons' diet (vertebrate meat eating and *A. senegal* leaf consumption: $r_s = -0.246$, $p = .440$, $N = 12$; insect eating and *A. senegal* leaf consumption: $r_s = -0.117$, $p = .716$, $N = 12$). The only significant relationship to emerge from these analyses was a positive correlation between insect eating and palm fruit consumption ($r_s = 0.627$, $p = .029$, $N = 12$).

We also found no relationship between insect consumption and monthly home range size ($r_s = -0.92$, $p = .788$, $N = 11$) or DPL ($r_s = 0.092$, $p = .788$, $N = 11$), nor between vertebrate meat eating and monthly home range size ($r_s = 0.303$, $p = .365$, $N = 11$) or DPL ($r_s = 0.321$, $p = .336$, $N = 11$). Similarly, neither the consumption of *H. thebaica* nor *A. senegal*—the two main contributors to the baboons' diet—were related to ranging patterns. There was no relationship between doum palm fruit consumption and either monthly home range size ($r_s = 0.041$, $p = .905$, $N = 11$) or DPL ($r_s = 0.114$, $p = .739$, $N = 11$). Similarly, we found no relationship between *A. senegal* leaf consumption and monthly home range size ($r_s = 0.236$, $p = .484$, $N = 11$) nor DPL ($r_s = -0.009$, $p = .979$, $N = 11$).

We found a significant negative relationship between monthly vertebrate meat eating rate and time spent feeding ($r_s = -0.606$, $p = .048$, $N = 12$), but no relationship between insect consumption and time spent feeding ($r_s = -0.064$, $p = .851$, $N = 12$). There was also no relationship between meat eating and time spent traveling (vertebrate meat eating: $r_s = 0.229$, $p = .497$, $N = 12$; insect-eating: $r_s = -0.275$, $p = .413$, $N = 12$).

Band 1 separated into independent clans for at least 37 days over the study period (a week in March and from mid-September to mid-October), on 15 of which we collected data. Only three of the 38 instances of vertebrate meat eating occurred when the band was separated into clans. Thus the rate of vertebrate meat eating did not differ based on group size (rate = 0.029/hr when the baboons functioned as a cohesive band; rate = 0.025/hr when they behaved as independent clans). Insects made up 0.7% of the diet when the

baboons functioned as a cohesive band and 1.2% when they remained as separate clans.

4 | DISCUSSION

Hamadryas baboons at Filoha were observed eating vertebrate prey 38 times in 1 year of observation (0.028/hr), an unusually high frequency of meat-eating compared with previous findings for this species and for baboons in general. Only olive baboons at Gilgil, Kenya consume vertebrates at higher rates (0.05/hr and 0.08/hr across two separate study periods; Strum, 1975). At Erer Gota, Ethiopia, the only other site at which hamadryas baboons have been observed continuously year-round, Kummer (1968) and Abegglen (1984) each observed only one instance of meat eating during study periods of the approximately 1 year each (0.001/hr and 0.002/hr, respectively), and neither directly observed predation. Neither predation nor consumption of vertebrates has been reported for the other hamadryas populations observed for shorter periods at Awash Station, Ethiopia (Nagel, 1973), Saudi Arabia (Biquand et al., 1992; Boug et al., 2017), Eritrea (Zinner et al., 2001), and Yemen (Al-Safadi, 1994). In addition to consuming a higher quantity of vertebrate meat than other hamadryas populations, the baboons at Filoha also consumed a greater diversity, with at least eight different prey species; this contrasts with the Erer Gota baboons, which were observed carrying only dead dik dik and rock hyrax (but not eating them).

The Filoha baboons spent 0.5% of their annual feeding budget consuming insects. This is comparable to olive baboons in Ivory Coast, for whom arthropods make up 0.8% of annual feeding records (Kunz and Linsemair, 2008), but is much lower than other baboons. In yellow baboons at Mikumi National Park, Tanzania, for example, the mean monthly percentage of insects in the diet is 19%, peaking at 40% (Rhine, 1986).

At Filoha, there was no sex difference in the consumption of either insects or vertebrate prey. While males were observed eating vertebrate meat more frequently than females, adults of both sexes, as well as juveniles, had access to vertebrate prey. We observed only one occasion in which an adult male prevented a female from feeding on meat by chasing her until she dropped the carcass. Similarly, one female prevented her leader male from eating meat by evading him and refusing to relinquish the meat. All age-sex classes (aside from dependent infants) thus had access to animal matter.

Overall, our hypothesis that seasonality in the availability and consumption of preferred plant foods would shape temporal patterns of meat eating at Filoha was not supported. Neither vertebrate meat nor insect-eating were associated with either rainfall or the consumption of *A. senegal* leaves, suggesting that the protein content of animal matter does not drive the consumption of meat. Furthermore, the relationship between meat eating and the consumption of palm fruit, another preferred plant food resource, was inconsistent. Instead, insect-eating was significantly positively related to doum palm fruit consumption, likely a chance outcome of

the timing of insect swarms. Taken together, these results suggest that the Filoha baboons do not rely on the animal matter as a seasonal substitute for either palm fruit or *A. senegal* leaves.

This overall lack of seasonal shift in meat eating at Filoha is consistent with other baboons. For example, yellow baboons in Mikumi National Park, Tanzania eat vertebrate meat throughout the year, at equal rates in the dry season and wet season (Rhine, 1986). Yellow baboons in Amboseli, Kenya, by contrast, eat more vertebrate meat during the dry season, perhaps to compensate for the lack of fresh vegetation or insects during this time (Hausfater, 1976). Seasonality of meat-eating appears to be more common in chimpanzees, which have been found at some sites to hunt more during the dry season (Stanford, 1996, 1998; Takahata, Hasegawa, & Nishida, 1984; Teleki, 1973); these studies, however, did not include data on the seasonal availability of fruit, precluding a true test of the nutritional shortfall hypothesis. More recent work has demonstrated that chimpanzees at Gombe in fact hunt more when diet quality is high (Gilby et al., 2006), chimpanzees at the Kanyawara site in Kibale National Park, Uganda hunt and eat more meat when preferred fruit species are abundant (Gilby & Wrangham, 2007), and chimpanzee hunting behavior at the Ngogo site in Kibale is positively correlated with fruit availability (Mitani & Watts, 2001; Watts & Mitani, 2002).

This pattern of increased hunting during periods of peak fruit availability makes sense for chimpanzees, as they actively patrol for prey at some sites, traveling long distances in search of red colobus monkeys (Mitani & Watts, 2001). The energetic costs of hunting colobus can be compensated for by the high fruit abundance during their peak hunting periods. Hamadryas baboons, on the other hand, do not actively pursue prey and instead hunt opportunistically during their regular daily travel. Thus, they do not incur additional energetic costs of meat eating that would necessitate the availability of high-energy foods, nor do they hunt in groups as do chimpanzees.

As an alternative hypothesis to seasonality, we hypothesized that the baboons' hunting habits may be a function of prey encounter rate and availability of time to pursue animal prey. The baboons' rate of vertebrate meat eating did increase significantly with less time spent feeding overall, suggesting that the pursuit of vertebrate prey is related to feeding time. There was no relationship, however, between time spent feeding and insect consumption. Similarly, neither consumption of vertebrate meat nor of insects was related to either home range size or distance traveled, suggesting that meat eating was not a simple function of the increased encounters with prey that would likely result from increased travel. The consumption of the two main food species in their diet, *H. thebaica* and *A. senegal*, was also unrelated to ranging patterns. These results suggest that neither reduced availability of preferred plant resources nor increased travel leading to more prey encounters drive the frequency of meat consumption.

As an additional link to prey encounter rate, we predicted that the consumption of animal matter would be related to subgrouping patterns. Our rationale for this prediction was that previous work at Filoha has shown the doum palm to be a critical resource at Filoha (Schreier, 2010; Swedell et al., 2008), likely allowing the larger band

and clan sizes seen at Filoha compared to elsewhere in hamadryas range (Schreier & Swedell, 2009, 2012; Swedell, 2002), and temporal patterns in palm fruit abundance to be linked to fission and fusion of social groupings. Band 1, for example, separates into independent clans for the longest periods of time during the time of year when palm fruit is not available (Schreier & Swedell, 2009, 2012), likely as a means to reduce scramble competition and ensure sufficient nutrient intake. The rate of vertebrate meat eating at Filoha, however, did not vary with band fissions. Although insects did contribute more to the baboons' diet when they were separated into independent clans than when they functioned as a cohesive band, this was primarily due to the presence of a swarm of dragonflies in March when palm fruit was also abundant. The baboons do not, therefore, appear to further compensate for increased feeding competition, beyond social fissioning, by supplementing their diet with meat, nor does foraging in smaller aggregations appear to increase their access to prey or likelihood of pursuing it.

Although there were no clear associations between vertebrate or insect-eating and the two main plant species in the baboons' diet, there was an inverse relationship between their consumption of vertebrate meat and that of insects. Over the course of the study period, the Filoha baboons alternated eating vertebrates and insects such that their diet included either one or the other every month of the year. The baboons, therefore, appear to maintain a small amount of animal matter in their diet year-round, likely providing them with low quantities of high-quality protein, micro-nutrients that are rare in their typical plant foods, and vitamin B-12 which they can only obtain from meat (Rothman, Raubenheimer, Bryer, Takahashi, & Gilbert., 2014). Vitamins and minerals are needed in only small amounts, and thus consuming a limited amount of animal matter throughout the year likely allows the baboons to maintain levels necessary to sustain them.

Although this study did not focus on the biology of prey species, the variation in both insect and vertebrate predation over the course of the study period is likely related at least in part to the distribution and abundance of these prey species. Almost all of the baboons' insect consumption occurred when swarms of locusts and dragonflies passed through the Filoha region, usually lasting a few consecutive days. These insects are generally solitary but sometimes become gregarious and travel in huge swarms consisting of millions of individuals, often following high levels of rainfall or other conditions that promote contact among individuals (Buhl et al., 2006; Simpson & Sword, 2008; Wikelski et al., 2006). We only observed a few instances of the insect-eating outside of such outbreaks, and we did not observe insect swarms on which the baboons did not feed. Given the large numbers of these insects during outbreaks, most band members simultaneously fed on them and predation success rate was high; if the baboons did not catch an insect when attempting to capture one, they could immediately try again. With vertebrate prey, on the other hand, after an unsuccessful predation attempt, it could be weeks or more before another opportunity arose. The dragonfly outbreaks followed several days of high rainfall; the

locust swarms, by contrast, all occurred during very dry periods with no clear impetus for the outbreaks. Future work at Filoha should be able to shed light on the presence of insect swarms in relation to environmental factors including rainfall, temperature, and distributions of plant foods to determine their predictability as baboon food resources.

The consumption of swarming insects by hamadryas at Filoha is consistent with that at other sites as well as with other primates more broadly. Hamadryas baboons at Erer Gota spent several hours feeding on locusts one morning when a large swarm settled close to their sleeping site (Kummer, 1968). Similarly, chacma baboons in the Namib desert, Namibia relied heavily on grasshoppers during an outbreak, substantially reducing daily travel to stay in the vicinity of these insects (Hamilton, Buskirk, & Buskirk, 1978). Altmann and Altmann (1970) report that yellow baboons at Amboseli also fed on grasshoppers, where predation was successful in 75% of attempts, consistent with high success rate at Filoha. Geladas (*Theropithecus gelada*) in Guassa, Ethiopia fed intensively on locusts during a several-day-long locust outbreak, while hardly consuming any insects at other times of the year (Fashing, Ngyuen, & Fashing, 2010). Bearded saki (*Chiropetes satanas*) insect consumption peaked with the presence of a large swarm of termites (Veiga & Ferrari, 2006). The presence of swarms thus appears to dictate insect-eating in many primates. Instead of actively pursuing these insects, the primates take advantage of their abundance opportunistically during outbreaks.

In contrast to insects, vertebrate prey at Filoha are not available in large aggregations but are instead encountered singly or in pairs. The baboons' most common prey, dik dik and Abyssinian hare, are both small mammals (~1–5 kg) that conceal themselves from predators in shrubs throughout their scrubland habitats (Flux & Angermann, 1990; Komers, 1996). Although the Filoha dik dik and hare populations have not been studied, dik dik are monogamous throughout their range and each pair defends a joint territory (Brotherton & Manser, 1997; Komers, 1996). Females give birth to one offspring at a time, usually once per year (Brotherton & Manser, 1997). Hare are solitary and breed year-round, producing several litters of 1–2 offspring each year (Flux & Angermann, 1990). The abundance of these prey species at Filoha did not appear to vary seasonally. Consistent with their small size, ability to blend into the environment, relatively low offspring production, and tendency to travel alone or in pairs, the Filoha baboons do not come across dik dik and hare especially frequently, and when they do, encounters are fleeting. Both species were preyed upon by the baboons across seven different months, each time in *Acacia* scrubland or open grassland habitats. Hare and dik dik may also range in palm forests in the Filoha region, but we did not observe them in these areas. Finally, while we did not systematically record encounters with potential prey or unsuccessful predation attempts, anecdotal evidence suggests that the baboons do not pursue vertebrate prey every time they are encountered. We observed just one unsuccessful predation attempt in which several baboons chased a jackal but could not catch it, but we cannot be certain there were no other such attempts.

Taken together, our results suggest that consumption of vertebrate prey is determined both by the underlying unpredictable nature of prey encounters and by available time. The baboons ate significantly more vertebrate meat the less time they spent feeding overall, suggesting that, regardless of how frequently the baboons encounter suitable vertebrate prey, they only actively chase it when they are not feeding on the plant resources more typical in their diet. An alternative explanation for the relationship between vertebrate prey consumption and time availability may be that the high-quality of vertebrate meat allows the baboons to spend less time feeding on other resources and yet still achieve the same nutrient intake. Overall, however, we cannot exclude the possibility that temporal and spatial patterns of prey availability are the primary driver of vertebrate predation at Filoha, as they are with insect predation.

Our results also reinforce the importance of the relationship between leader males and their females in hamadryas society. Of the two instances in which meat was consumed by two baboons simultaneously, it was between a leader male and one of the females in his OMU. Cofeeding between leader males and OMU females, or passive meat sharing, also occurs in Guinea baboons (Goffe & Fischer, 2016). Both hamadryas and Guinea baboons are characterized by multi-level societies based on one-male units in which male-female bonds are stronger than in other baboons, and consequently both taxa have been proposed as models for the evolution of hominin behavior (Swedell and Plummer, 2012; Fischer et al., 2017; Goffe, Zinner, & Fischer, 2016).

Any interpretations from the results of this study should be considered preliminary because data on insect and vertebrate eating were collected via different methods, and thus results regarding their consumption are not wholly comparable. The baboons fed on insects primarily during swarms when most members of the band simultaneously chased, caught, and ate insects. Because we collected data on focal OMUs, we were recording feeding by only a small proportion of the band at a time, that is, the leader male of our focal OMU and his female(s), and our results, therefore, under-represent the intensity of insect consumption. On the other hand, we collected data on vertebrate predation via ad libitum sampling of the entire study band, and thus it is likely that we missed some instances of vertebrate meat eating by some members of the band when we were observing others (Rhine, 1986). Band 1 comprised more than 200 baboons who spread out, on average, across 220 m, but sometimes as far as 700 m (Schreier & Swedell, 2012). With only two observers at any given time, our vertebrate meat-eating results likely underestimate the rate of consumption (Rhine, 1986).

Despite these limitations, our results suggest that animal matter is an important component of the diet of Filoha baboons. We found an inverse relationship between insect eating and vertebrate consumption, such that the baboons maintain a small amount of animal matter in their diet year-round. Insect consumption appears to be driven by the presence of swarms of locusts and dragonflies, whereas the consumption of vertebrate prey probably relates to both prey abundance and distribution and availability of feeding time. In both cases, the animal matter is not actively sought by the baboons,

but they readily consume it when opportunities arise and when time allows. Future work at Filoha on patterns of meat eating in relation to time spent feeding and the presence and distribution of insect and vertebrate prey can address whether this pattern holds across years and provides the baboons with an effective strategy for maintaining a consistent amount of high-quality protein in their diet throughout the year.

ACKNOWLEDGEMENTS

We thank the Ethiopian Wildlife Conservation Authority for permission to conduct research at Filoha and the staff of Awash National Park for facilitating this study. Funding for this research was provided by the City University of New York PSC-CUNY Research Award Program (award #66588-0035 to L. Swedell), the New York Consortium in Evolutionary Primatology, and the City University of New York PhD Program in Anthropology. For assistance and support in the field, we are grateful to Teklu Tesfaye, Demekech Woldearegay, Tariku Woldearegay, Getu Mamush, Denberu Tesfaye, Getu Kifle, Getenet Hailemeskel, Christine Tuillon, and Matt Klein. For statistical guidance, we thank Kristofor Voss.

ORCID

Amy L. Schreier  <http://orcid.org/0000-0002-0379-3750>

Larissa Swedell  <http://orcid.org/0000-0001-6909-2669>

REFERENCES

- Abegglen, J. J. (1984). *On socialization in hamadryas baboons: A field study*. London: Associated University Presses.
- Aboshora, W., Lianfu, Z., Dahir, M., A.a gasmalla, M., Musa, A., Omer, E., & Thapa, M. (2014). Physiochemical, nutritional and functional properties of the epicarp, flesh and pitted sample of doum fruit (*Hyphaene thebaica*). *Journal of Food Nutrition Resources*, 2, 180–186. <https://doi.org/10.12691/jfnr-2-4-8.1>
- Al-Safadi, M. M. (1994). The hamadryas baboon, *Papio hamadryas* (Linnaeus, 1758) in Yemen (Mammalia: Primates: Cercopithecidae). *Zoology in the Middle East*, 10, 5–16. <https://doi.org/10.1080/09397140.1994.10637655>
- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49, 227–265.
- Altmann, S. A., & Altmann, J. (1970). *Baboon ecology*. Chicago: University of Chicago Press.
- Biquand, S., Biquand-Guyot, V., Boug, A., & Gautier, J. P. (1992). Group composition in wild and commensal hamadryas baboons: A comparative study in Saudi Arabia. *International Journal of Primatology*, 13, 533–543.
- Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology*, 78, 547–573. <https://doi.org/10.1002/ajpa.1330780410>
- Boug, A., Zafar-ul Islam, M., Iwamoto, T., Mori, A., Yamane, A., & Schreier, A. L. (2017). The relationship between artificial food supply and natural food selection in two troops of commensal hamadryas baboons in Saudi Arabia. *Journal of Threatened Taxa*, 9, 10741–10756. <https://doi.org/10.11609/jott.3348.9.10.10741-10756>
- Brotherton, P. N. M., & Manser, M. B. (1997). Female dispersion and the evolution of monogamy in the dik-dik. *Animal Behaviour*, 54, 1413–1424. <https://doi.org/10.1006/anbe.1997.0551>
- Buckley, B. J. W., Dench, R. J., Morrough-Bernard, H. C., Bustani, U., & Chivers, D. J. (2015). Meat eating by a wild Bornean orang-utan (*Pongo pygmaeus*). *Primates*, 56, 293–299. <https://doi.org/10.1007/s10329-015-0487-x>
- Buhl, J., Sumpter, D. J. T., Couzin, I. D., Hale, J. J., Despland, E., Miller, E. R., & Simpson, S. J. (2006). From disorder to order in marching locusts. *Science*, 312, 1402–1406. <https://doi.org/10.1126/science.1125142>
- Cardoso Coimbra, M., & Jorge, N. (2011). Characterization of the pulp and kernel oils from *Syagrus oleracea*, *Syagrus romanzoffiana*, and *Acrocomia aculeata*. *Journal of Food Science*, 76, 1156–1161. <https://doi.org/10.1111/j.1750-3841.2011.02358.x>
- Chapman, C. A., Rothman, J. M., & Lambert, J. E. (2012). Food as a selective force in primates. In J. C. Mitani, J. Call, P. Kappeler, R. A. Palombit, & J. B. Silk (Eds.), *Evolution of primate societies* (pp. 149–168). Chicago: University of Chicago Press.
- Cords, M. (1986). Interspecific and intraspecific variation in the diet of two forest guenons, *Cercopithecus ascanius* and *Cercopithecus mitis*. *Journal of Animal Ecology*, 55, 811–827.
- Davidge, C. (1978). Ecology of baboons (*Papio ursinus*) at Cape Point. *Zoologica Africana*, 13, 329–350. <https://doi.org/10.1080/00445096.1978.11447633>
- Davies, J. G., & Cowlshaw, G. (1996). Baboon carnivory and raptor interspecific competition in the Namib Desert. *Journal of Arid Environments*, 34, 247–249. <https://doi.org/10.1006/jare.1996.0106>
- Deblauwe, I. (2009). Temporal variation in insect-eating by chimpanzees and gorillas in southeast Cameroon: Extension of niche differentiation. *International Journal of Primatology*, 30, 229–252. <https://doi.org/10.1007/s10764-009-9337-2>
- Deblauwe, I., & Jannsens, G. P. J. (2008). New insights in insect prey choice by chimpanzees and gorillas in Southeast Cameroon: The role of nutritional value. *American Journal of Physical Anthropology*, 135, 42–55. <https://doi.org/10.1002/ajpa.20703>
- Fashing, P. J., Ngyuen, N., & Fashing, N. J. (2010). Behavior of geladas and other endemic wildlife during a desert locust outbreak at Guassa, Ethiopia: Ecological and conservation implications. *Primates*, 51, 193–197. <https://doi.org/10.1007/s10329-010-0194-6>
- Fischer, J., Kopp, G. H., Dal Pesco, F., Goffe, A., Hammerschmidt, K., Kalbitzer, U., & Zinner, D. (2017). Charting the neglected West: The social system of Guinea baboons. *American Journal of Primatology*, 162, 15–31. <https://doi.org/10.1002/ajpa.23144>
- Flux, J. E. C., & Angermann, R. (1990). The hares and jackrabbits. In A. Chapman, & J. E. C. Flux (Eds.), *Rabbits, hares and pikas: status survey and conservation action plan* (pp. 61–92). Gland, Switzerland: IUCN Lagomorph Specialist Group.
- Ganas, J., & Robbins, M. M. (2004). Intrapopulation differences in ant eating in the mountain gorillas of Bwindi Impenetrable National Park, Uganda. *Primates*, 45, 275–278. <https://doi.org/10.1007/s10329-004-0089-5>
- Gilby, I. C., Eberly, L. E., Pintea, L., & Pusey, A. E. (2006). Ecological and social influences on the hunting behaviour of wild chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour*, 72, 169–180. <https://doi.org/10.1016/j.anbehav.2006.01.013>
- Gilby, I. C., & Wrangham, R. W. (2007). Risk-prone hunting by chimpanzees (*Pan troglodytes schweinfurthii*) increases during periods of high diet quality. *Behavioral Ecology and Sociobiology*, 61, 1771–1779. <https://doi.org/10.1007/s00265-007-0410-6>
- Goffe, A. S., & Fischer, J. (2016). Meat sharing between male and female Guinea baboons (*Papio papio*). *Primate Biology*, 3, 1–8. <https://doi.org/10.5194/pb-3-1-2016>
- Goffe, A. S., Zinner, D., & Fischer, J. (2016). Sex and friendship in a multilevel society: Behavioral patterns and associations between female and male Guinea baboons. *Behavioral Ecology and Sociobiology*, 70, 323–336. <https://doi.org/10.1007/s00265-015-2050-6>

- Hamilton, W. J., III, Buskirk, R. E., & Buskirk, W. H. (1978). Omnivory and utilization of food resources by chacma baboons, *Papio ursinus*. *American Naturalist*, 112, 911–924.
- Hamilton, W. J., III, & Busse, C. D. (1978). Primate carnivory and its significance to human diets. *BioScience*, 28, 761–766. <https://doi.org/10.2307/1307249>
- Hausfater, G. (1976). Predatory behavior of yellow baboons. *Behaviour*, 56, 44–68. <https://doi.org/10.1163/156853976X00299>
- Hoebekke, P. (1989). *The Turkana Doum Palm (Hyphaene compressa) as a Biological Resource in Turkana, Kenya*. Norway: University of Trondheim. M.Sc. Thesis.
- Komers, P. E. (1996). Obligate monogamy without paternal care in Kirk's dik dik. *Animal Behaviour*, 51, 131–140. <https://doi.org/10.1006/anbe.1996.0011>
- Kummer, H. (1968). *Social organization of hamadryas baboons: A field study*. Chicago: University of Chicago Press.
- Lambert, J. (2011). Primate nutritional ecology: Feeding biology and diet at ecological and evolutionary scales. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. M. Stumpf (Eds.), *Primates in perspective* (pp. 512–522). New York: Oxford University press.
- Kunz, B. K., & Linsenmair, K. E. (2008). The disregarded west: Diet and behavioural ecology of olive baboons in the ivory coast. *Folia Primatologica*, 79, 31–51.
- Lewis, M. C., & O'Riain, M. J. (2017). Foraging profile, activity budget and spatial ecology of exclusively natural-foraging chacma baboons (*Papio ursinus*) on the Cape Peninsula, South Africa. *International Journal of Primatology*, 38, 751–779.
- Lewis, M. C., West, A. G., & O'Riain, M. J. (2018). Isotopic assessment of marine food consumption by natural-foraging chacma baboons on the Cape Peninsula, South Africa. *American Journal of Physical Anthropology*, 165, 77–93. <https://doi.org/10.1002/ajpa.23332>
- Lokuruka, M. N. I. (2007). Amino acids and some minerals in the nut of the Turkana doum palm (*Hyphaene coriacea*). *African Journal of Food, Agriculture, Nutrition, and Development ONLINE*, 7. <http://www.ajfand.net/Issue13/PDFs/Lokuruka-2005.pdf>
- Milton, K. (2003). Micronutrient intakes of wild primates: Are humans different? *Comparative Biochemistry and Physiology A*, 136, 47–59. [https://doi.org/10.1016/S1095-6433\(03\)00084-9](https://doi.org/10.1016/S1095-6433(03)00084-9)
- Mitani, J. C., & Watts, D. P. (2001). Why do chimpanzees hunt and share meat? *Animal Behaviour*, 61, 915–924.
- Nagel, U. (1973). A comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. *Folia Primatologica*, 19, 104–165.
- Ostro, L. E. T., Young, T. P., Silver, S. C., & Koontz, F. W. (1999). A Geographic Information System method for estimating home range size. *Journal of Wildlife Management*, 63, 748–755. <https://doi.org/10.2307/3802665>
- Rhine, R. J. (1986). Insect and meat eating among infant and adult baboons (*Papio cynocephalus*) of Mikumi National Park, Tanzania. *American Journal of Physical Anthropology*, 70, 105–118.
- Rose, L. M. (1997). Vertebrate predation and food-sharing in *Cebus* and *Pan*. *International Journal of Primatology*, 18, 727–765. <https://doi.org/10.1023/A:1026343812980>
- Rose, L. M., Perry, S., Panger, M. A., Jack, K., Manson, J. H., Gros-Louis, J., ... Vogel, E. (2003). Interspecific interactions between *Cebus capucinus* and other species: Data from three Costa Rican sites. *International Journal of Primatology*, 24, 759–796. <https://doi.org/10.1023/A:1024624721363>
- Rothman, J. M., Raubenheimer, D., Bryer, M. A. H., Takahashi, M., & Gilbert, C. C. (2014). Nutritional contributions of insects to primate diets: Implications for primate evolution. *Journal of Human Evolution*, 71, 59–69. <https://doi.org/10.1016/j.jhevol.2014.02.016>
- Schreier, A., & Swedell, L. (2008). Use of palm trees as a sleeping site by hamadryas baboons (*Papio hamadryas hamadryas*) in Ethiopia. *American Journal of Primatology*, 70, 107–113. <https://doi.org/10.1002/ajp.20465>
- Schreier, A. L. (2010). Feeding ecology, food availability, and ranging patterns of wild hamadryas baboons at Filoha. *Folia Primatologica*, 81, 129–145. <https://doi.org/10.1159/000316562>
- Schreier, A. L., & Swedell, L. (2009). The fourth level of social structure in a multi-level society: Ecological and social functions of clans in hamadryas baboons. *American Journal of Primatology*, 71, 948–955. <https://doi.org/10.1002/ajp.20736>
- Schreier, A. L., & Swedell, L. (2012). Ecology and sociality in a multilevel society: Ecological determinants of social cohesion in hamadryas baboons. *American Journal of Physical Anthropology*, 148, 580–588. <https://doi.org/10.1002/ajpa.22076>
- Sigg, H., & Stolba, A. (1981). Home range and daily march in a hamadryas baboon troop. *Folia Primatologica*, 26, 40–75. <https://doi.org/10.1159/000156008>
- Simpson, S. J., & Sword, G. A. (2008). Locusts. *Current Biology*, 18, 364–366.
- Stanford, C. B. (1994). Hunting decisions in wild chimpanzees. *Behaviour*, 131, 1–18. <https://doi.org/10.1163/156853994X00181>
- Stanford, C. B. (1996). The hunting ecology of wild chimpanzees: Implications for the evolutionary ecology of Pliocene hominids. *American Anthropologist*, 98, 96–113. <https://doi.org/10.1525/aa.1996.98.1.02a00090>
- Stanford, C. B. (1998). *Chimpanzee and red colobus: The ecology of predator and prey*. Cambridge, MA: Harvard University Press.
- Stanford, C. B. (2008). *Apes of the Impenetrable Forest: The behavioral ecology of sympatric chimpanzees and gorillas*. Upper Saddle River, NJ: Pearson.
- Strum, S. C. (1975). Primate predation: Interim report on the development of a tradition in a troop of olive baboons. *Science*, 187, 755–757. <https://doi.org/10.1126/science.187.4178.755>
- Strum, S. C. (1983). Baboon cues for eating meat. *Journal of Human Evolution*, 12, 327–336. [https://doi.org/10.1016/S0047-2484\(83\)80159-6](https://doi.org/10.1016/S0047-2484(83)80159-6)
- Swedell, L. (2002). Ranging behavior, group size and behavioral flexibility in Ethiopian hamadryas baboons (*Papio hamadryas hamadryas*). *Folia Primatologica*, 73, 95–103. <https://doi.org/10.1159/000064787>
- Swedell, L. (2006). *Strategies of sex and survival in hamadryas baboons: Through a female lens*. Upper Saddle River, NJ: Prentice Hall College Division.
- Swedell, L., & Tesfaye, T. (2003). Infant mortality after takeovers in wild Ethiopian hamadryas baboons. *American Journal of Primatology*, 60, 113–118. <https://doi.org/10.1002/ajp.10096>
- Swedell, L., & Plummer, T. (2012). A papionin multilevel society as a model for hominin social evolution. *International Journal of Primatology*, 33(5), 1165–1193.
- Swedell, L., Hailemeskel, G., & Schreier, A. (2008). Composition and seasonality of diet in wild hamadryas baboons: Preliminary findings from Filoha. *Folia Primatologica*, 79, 476–490. <https://doi.org/10.1159/000164431>
- Takahata, Y., Hasegawa, T., & Nishida, T. (1984). Chimpanzee predation in the Mahale Mountains from August 1979 to May 1982. *International Journal of Primatology*, 5, 213–233. <https://doi.org/10.1007/BF02735758>
- Tashiro, Y. (2006). Frequent insectivory by two guenons (*Cercopithecus lhoesti* and *Cercopithecus mitis*) in the Kalinzu Forest, Uganda. *Primates*, 47, 170–173. <https://doi.org/10.1007/s10329-005-0160-x>
- Teleki, G. (1973). *The predatory behavior of wild chimpanzees*. Lewisburg, PA: Bucknell University Press.
- Tennie, C., O'Malley, R. C., & Gilby, I. C. (2014). Why do chimpanzees hunt? Considering the benefits and costs of acquiring and consuming vertebrate versus invertebrate prey. *Journal of Human Evolution*, 71, 38–45. <https://doi.org/10.1016/j.jhevol.2014.02.015>

- Veiga, L. M., & Ferrari, S. F. (2006). Predation of arthropods by southern bearded sakis (*Chiroptes satanas*) in Eastern Brazilian Amazonia. *American Journal of Primatology*, 68, 209–215. <https://doi.org/10.1002/ajp.20217>
- Watts, D. P., & Amsler, S. J. (2013). Chimpanzee-red colobus encounter rates show a red colobus population decline associated with predation by chimpanzees at Ngogo. *American Journal of Primatology*, 75, 927–937. <https://doi.org/10.1002/ajp.22157>
- Watts, D. P., & Mitani, J. C. (2002). Hunting behavior of chimpanzees at Ngogo Kibale National Park, Uganda. *International Journal of Primatology*, 23, 1–28. <https://doi.org/10.1023/A:101327060>
- Whiten, A., Byrne, R. W., Barton, R. A., Waterman, P. G., & Henzi, S. P. (1991). Dietary and foraging strategies of baboons. *Philosophical Transactions of the Royal Society B*, 334, 187–197. <https://doi.org/10.1098/rstb.1991.0108>
- Whiten, A., Byrne, R. W., & Henzi, S. P. (1987). The behavioral ecology of mountain baboons. *International Journal of Primatology*, 8, 367–388. <https://doi.org/10.1007/BF02737389>
- Wikelski, M., Moskowicz, D., Adelman, J. S., Cochran, J., Wilcove, D. S., & May, M. (2006). Simple rules guide dragonfly migration. *Biology Letters*, 2, 325–329. <https://doi.org/10.1098/rsbl.2006.0487>
- Williamson, C. S., Foster, R. K., Stanner, S. A., & Buttriss, J. L. (2005). Red meat in the diet. *Nutrition Bulletin*, 30, 323–355. <https://doi.org/10.1111/j.1467-3010.2005.00525.x>
- Zinner, D., Peláez, F., & Torkler, F. (2001). Distribution and habitat associations of baboons (*Papio hamadryas*) in Central Eritrea. *International Journal of Primatology*, 22, 397–413. <https://doi.org/10.1023/A:101070361>

How to cite this article: Schreier AL, Schlaht RM, Swedell L. Meat eating in wild hamadryas baboons: Opportunistic trade-offs between insects and vertebrates. *Am J Primatol*. 2019;e23029. <https://doi.org/10.1002/ajp.23029>