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Cognition, foraging, and energetics in extant and extinct primates

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Cognition, foraging, and energetics in extant and extinct primates

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Editorial: Cognition, foraging, and energetics in extant and extinct primates

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Editorial on the Research Topic
Cognition, foraging, and energetics in extant and extinct primates

Within the framework of optimal foraging theory (Stephens and Krebs, 1986; Pyke, 2019), primates living in complex and fluctuating environments are likely to mobilize cognitive skills—such as episodic or long-term memory, planning and value-based decision-making—that allow them to exhibit more efficient foraging decisions and strategies (Janson, 2019; Trapanese et al., 2019; Garcia et al., 2021). These strategies toward optimizing energetic balance (i.e., maximizing benefits while minimizing costs and risks associated with the exploitation of resources in the environment) are suggested to vary at the interspecific level but also to be constrained—or indeed enhanced—by the social context.

Nevertheless, there is still much we do not know about the cognition supporting foraging behavior in primates, and a collective and concerted effort toward filling the gaps was needed. This Research Topic has brought together researchers from diverse disciplines including animal cognition, behavioral ecology, paleoanthropology, archeology, and ethnoecology. It aimed to illustrate our current understanding of the diversity in primate foraging strategies and associated cognitive abilities in different socio-ecological contexts, both past and present. The issue is composed of contributions on modern primates (including humans) as well as extinct hominins, from laboratory settings and from fieldwork, and taking empirical, theoretical, or conceptual approaches to provide a more complete understanding of foraging cognition across the primate order. Overall, these studies highlight the extraordinary variation existing in several key cognitive processes mobilized for foraging, and point to socio-ecological factors that drive the evolution of foraging decisions at the individual and collective levels. Foraging behaviors draw on cognitive skills to make complex decisions (e.g., in modulating navigation strategies or travel paths for exploiting sparse or ephemeral resources: Janmaat et al., 2014; Green et al., 2020) contingent on ecological challenges but also on long-lasting social interactions with competing or cooperating conspecifics (see Garcia et al., 2021 for a review). Four articles in our collection illustrate the complexity of foraging decisions related to the optimization of cost-benefit ratios.

Two focus on "high-yield, high-risk" resources, e.g., aquatic resources and meat fat, both hypothesized to have played significant roles in human evolution (Snodgrass et al., 2009; Cunnane and Stewart, 2010). In their review, de Chevalier et al. suggest that aquatic foraging could have emerged in several non-human primate species at sites where the local cost-benefit trade-offs favor aquatic vs. terrestrial food items. Moreover, they suggest that the unique intensification of aquatic resource consumption in hominins has led to true coastal adaptations, expansion of their niches and diversification of their diets. In another paper, Daujeard and Prat review the costs and benefits of meat and fat consumption during the course of human evolution, in terms of energetic impact and social aspects (social cooperation, food sharing). They also point out the difficulties and limits encountered in this research area, notably by the scarcity of archeological evidence but also by the silent influences of culture and symbolism on food choices. A third article (Gallois and Henry) explores the costs of activities related to gathering and plant foods acquisition in the livelihood of a mixed economy society, the Baka forager-horticulturalists in Cameroon. They show that gathering activities are energetically costly, with higher energy expenditures than for hunting and fishing activities, and that the costs associated with gathering depend on the targeted plant foods. Finally, by using an experimental approach in wild vervet monkeys, Arseneau-Robar et al. show that these monkeys make foraging decisions based on a balancing of costs and benefits, i.e., minimizing travel time and distance, but also ensuring they get access to their preferred food rewards when competitors are present. By taking into account complex social contexts in the planning of their foraging trips, they are capable of quickly assessing the risk of competition and modifying their route accordingly, showcasing the impressive complexity of foraging decisions in this species.

Three further papers provide detailed examinations of food-related decision-making in both human and non-human primates. Such decisions can be crucial components of fitness: detecting, discriminating, and efficiently exploiting known resources are fundamental skills for survival. At the same time, identifying novel food items can not only buffer individuals in times of low resource availability, but also potentially provide individuals with a selective advantage over others in the population, particularly when environments change and novel foods appear while familiar sources disappear (Webster and Lefebvre, 2001; Amici et al., 2020).

In this vein, Ventricelli et al. experimentally examine captive capuchins' responses to novel foods, predicting that neophobia toward these items will vary according to three distinct effects: experience, risk-aversion, and social rank. While none of these effects materializes in the data, the study does highlight effects of social rank and sex on neophobia. These likely relate to the nature of competitive interactions around both familiar and novel foods in the experiment, and have implications for the dynamics of incorporating novel foods into the dietary repertoire of wild populations. Shifting to the wild, Matsuda et al. examine food selectivity in guerezas in Uganda and show that neither the chemical and mechanical properties of leaves, nor their digestibility and abundance influence the guerezas' choices. However, they do identify differences in foraging effort devoted to leaves based on their protein content and toughness. Examining related questions in humans, Veen et al. report on the foraging behavior of Mbendjele BaYaka forager children in the Republic of the Congo. In contrast to the diet of other primates, the human diet is characterized by a diverse variety of high-quality and difficult-to-acquire foods (Milton, 1999; Kaplan et al., 2000). The authors find that BaYaka chilDren are able, already from an early age, to correctly identify foraging related plant species, and their botanical knowledge increases with age. Furthermore, they exhibit early sex-related specialization in foraging skills. Crucially, the study also documents how the diet of the BaYaka is changing along with their increasingly horticultural lifestyle, further highlighting that the effects that such shifts may have on the development of children's spatial and foraging cognition are as yet unknown.

Finally, two papers in our collection review some of the unique foraging challenges associated with the primate lifestyle. Harel et al. outline how moving through canopy environments makes specific demands on individuals' sensory, cognitive, and locomotory skills. The "networks of branching pathways" they need to negotiate in order to travel between destinations require individuals to weigh up the risks, costs, and rewards of multiple available options. The authors further highlight that the structure of canopy environments may also influence primate groups' capacity for coordinated action and cohesion, phenomena that become central in Williams et al.'s extensive review. This contribution provides an overview of the impact that sociality and the need for collective action may have on how primates tackle foraging challenges. Moving and foraging in groups is associated with increased competition, exacerbated by dominance asymmetries, leading to inequalities, intra-group conflict, and the differential balancing of benefits and costs across group members. Yet, through both democratic and despotic inputs, collective behavior can be highly efficient under many circumstances. The authors draw analogies with research in human organizational psychology to encourage a better understanding of the effect of group size and group composition on collective decision-making, collective movement, leadership, knowledge pooling, and coordinated action.

Together, our nine contributions showcase the diversity in primate foraging strategies and associated cognitive abilities, painting a nuanced picture for what foraging cognition is. Such work has opened new exciting questions that merit investigation and we hope that the contributions contained within this special issue will stimulate discussion and promote more research. Given ongoing habitat destruction and globalization (Estrada et al., 2017), one can wonder what the consequences will be of the decrease in species diversity and required botanical knowledge on the cognitive development of modern human foragers as well as other primates.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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The Cost of Gathering Among the Baka Forager-Horticulturalists From Southeastern Cameroon

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What present-day foragers do for their living and what they eat have long been privileged areas for exploring human behavior, global health, and human evolution. While many studies have focused on hunting and meat acquisition, less attention has been given to gathering and plant foods. Despite evidence of variation in both nutritional quality and energetic costs of gathering different plants, the overall effort spent on gathering in relation to other subsistence tasks is still under explored. In the current context of economic, climate, and social changes, many forager societies also rely on other subsistence strategies, including agriculture and wage labor. In this study, we aim to explore the place of gathering in the livelihood of a mixed economy society, the Baka forager-horticulturalists of southeastern Cameroon, by comparing the involvement and the costs of activities related to food acquisition. From a pool of 153 adult participants (97 women and 56 men), we collected 246 daily records using a GPS (Global Positioning System) tracker combined with heart rate monitor and time allocation recalls. We compared the duration, distance traveled, and the intensity of work, measured by calculating the metabolic equivalent of task (MET), of subsistence activities related to food acquisition. Results from this work show that gathering activities, performed by both women and men, are energetically costly, with higher MET values than hunting and fishing activities. Furthermore, the MET values vary depending on the targeted plant foods. We discuss these insights in the overall framework of subsistence patterns, merging them with the socio-cultural and environmental factors that might explain Baka livelihood and subsistence strategy.

Keywords: food choice, wild edible plants, energy expenditure, MET, hunter-gatherers

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INTRODUCTION

The livelihood and subsistence patterns of human groups have been studied from a variety of viewpoints, often with the goal of finding universal patterns or drivers of behavior. Insights from such research are used to build economic theories, to explain global health patterns, and even to create models of human evolution (Cordain et al., 2005; Hawkes et al., 2017; Widlok, 2017; Veile, 2018). Hunter-gatherer groups are of particular interest, as foraging subsistence patterns are thought to define 99% of human history (Crittenden and Schnorr, 2017). Subsistence behaviors, and the related social structures such as the gendered and age-related division of labor, egalitarianism and the high rate of sharing seen among hunter-gatherers (Hewlett, 2014), are often considered to represent fundamental human patterns (Marlowe, 2007; Codding and Kramer, 2016). However, there is a great deal of variation both between and within foraging societies in how subsistence tasks are performed (e.g., Kelly, 1995). Men tend to spend more time and energy on hunting and women on gathering (Gurven and Hill, 2009) and men cover greater distances than women for acquiring food (Pontzer and Wood, 2021; Wood et al., 2021). Subsistence activities also vary across age categories, with children and adults focusing on different resources (Gallois, 2017), and elders dedicating more time to activities other than food acquisition, such as childcare and knowledge transmission (Kaplan et al., 2000).

Most research on subsistence has focused primarily on the acquisition of meat, with less attention given to gathering and plant foods (e.g., Lee and DeVore, 1973; Cordain et al., 2002; Sillitoe, 2002). This bias is due in part to the emphasis on animal foods both assumed by the researcher and expressed by certain forager groups. Economic models such as optimal foraging theory emphasize the higher caloric returns of meat over other foods (Hawkes et al., 1982), and some hunter-gatherer groups, such as the Hadza of Tanzania, the Ache of Paraguay, and the Hiwi of Venezuela, rely heavily on animal foods (Kaplan et al., 2000). Moreover, socio-cultural investigations reflect the stated importance and preferences for animal foods (Motte-Florac et al., 1996) and prestige signaling opportunities (show-off behavior) associated with hunting (Gurven and von Rueden, 2006). In contrast, gathering as a fundamental human pattern is still underexplored, even if it might be a predominant activity among several hunter-gatherer societies (Dahlberg, 1981; Kelly, 1995). Furthermore, wild plants play a major role in providing micronutrients and ensuring food security (Pontzer and Wood, 2021). Evidence indicates great differences in nutritional quality and energetic costs for gathering diverse plant foods (Hladik, 1996; Paine et al., 2019). Their abundance and distribution across the landscape also differ, which contributes to varying travel distances and therefore time and energy spent while foraging (Wood et al., 2021). Despite this variation among gathered resources, "gathering" is often considered only as a single, homogenous category (e.g., Hurtado et al., 1985; Gurven and Kaplan, 2006). Therefore, carefully quantifying the costs of gathering compared to other subsistence tasks such as hunting, fishing and farming, and exploring the intrinsic variability in costs among different wild resources might provide us with relevant insights on an understudied component of human foraging behaviors.

Worldwide, hunter-gatherer societies are increasingly faced with challenges to their culture and livelihood through processes such as market integration, influence of the "mainstream" culture, and local environment degradation. These influences lead many to adopt other subsistence strategies, such as agriculture and wage labor (Codding and Kramer, 2016; Reyes-García and Pyhälä, 2017). Such changes have also led to a process of dietary transitions with a decrease in the consumption of wild foods and greater use of processed foods (Kuhnlein, 2015; Reyes-García et al., 2019), which has consequences for the health of these societies (Kuhnlein, 2015). This transition is not a single unidirectional process, and several societies maintain hunting and gathering while relying on other subsistence activities (Codding and Kramer, 2016). It remains unclear, however, how these dietary changes might alter gathering practices.

With this study, we aimed to fill these gaps by exploring the role of gathering wild foods in the livelihood of a hunter-gatherer society exposed to socio-ecological changes. We worked with the Baka, a group of forager-horticulturalists from southeastern Cameroon, who combine hunting and gathering with growing a small number of crops, and working for the neighboring Bantu-speaking farmers. To explore the role of gathering among the Baka, we posed the following research questions: (1) How do the Baka engage in the different activities related to food acquisition and how is their time allocation in subsistence activities related to the gender and the age of the individuals, and to their settlement (village vs. forest camp)? (2) Do the different subsistence activities vary in terms of intensity of effort, duration of work, and distance traveled? Are the variations in intensity, duration, and distance of these activities driven by the gender, the age or the settlement of the individuals? (3) Is gathering a uniform subsistence type, or do the intensity, duration and distance vary depending on the types of food gathered?

THE BAKA

The Baka live in the tropical forest of the Congo Basin across the Republic of Congo, Gabon, Central African Republic, and Cameroon, with a population of about 30,000 individuals (Leclerc, 2012). They were formerly a nomadic society, mostly living on hunting, gathering, fishing, and bartering products with their neighbors, sedentary Bantu-speaking farmers. Since the 1950s the Baka in Cameroon have shifted from a hunter-gatherer to a more forager-farmer livelihood through a process of sedentarization along the logging roads and adoption of agriculture (Leclerc, 2012). These permanent settlements, usually close to those of their farming neighbors, have provided them increased access to schools and health services, and a broader market, due to the presence of shops and the visits of merchants and traders of forest products. In addition, ecological changes due to deforestation and land degradation, the increasing arrival of external actors (loggers, traders of bushmeat and forest products), and also the establishment of conservation areas have reduced Baka's access to land and to natural resources as they do not have any land tenure.

Today the Baka engage not only in subsistence activities including hunting, gathering, fishing, and cultivating crops in agricultural fields (either their own or those of the Bantu), but also in economic activities such as selling forest products and wage labor for logging companies, Bantu-speaking farmers, or other outside groups coming from other areas in Cameroon. Most of the food consumed by the Baka, particularly the staples such as cassava (*Manihot esculenta*) and plantain (*Musa x paradisiaca*), come from the agricultural fields (Reyes-García et al., 2019; Gallois et al., 2020). However, a variety of key nutrients come from forest foods, including protein from wild game and fish, fat from nuts, and other important non-caloric nutrients from a large number of wild plants (Gallois et al., 2020).

The Baka use a variety of forest foods in their meal: wild tubers (mostly from *Dioscorea* spp.) are the often the main source of carbohydrates, leaves and mushrooms are added to the main dish, and oils from nuts, particularly palm nuts and *Irvingia* spp. are used for cooking and providing fat. Other products are consumed separately from the main meal, including palm wine made from the pith of *Raphia* spp. and honey produced by a variety of different bees, including *Apis mellifera*, and several species of stingless bees from the Meliponini tribe.

The Baka have a high level of expert knowledge about forest resources that they use for food, medicine, and shelter (i.e., house building and maintenance) (Bahuchet, 1992; Dounias, 2001; Hattori, 2006). More than 100 different wild edible plants are known and used by the Baka (Gallois et al., 2020), and the wild yams (*Dioscorea* spp., see Gallois et al., 2020 for the IDs) are the best-studied examples of Baka's plant knowledge (Dounias, 2001). Despite their challenging nature – they are difficult to find and dig up (Sato et al., 2012) – the Baka have developed sophisticated techniques to make use of these key starchy resources, including harvesting methods that encourage regrowth (Dounias, 2001), and even transplanting them in their own fields. Beyond nutrition, these plants also appear as key elements of their cosmology and relationship to both the forest and the elephant (Dounias, 2001).

The Baka's relationship with their food resources is changing, however, due to sedentarization, dietary transitions, and the increasing consumption of drugs and alcohol, all of which have considerable impacts on Baka culture, social cohesion and health (Dounias and Froment, 2006; Gallois et al., 2020). Settlements that are close to market towns show stronger effects of such influences (Carson et al., 2019), including considerable changes in how they acquire their food. For example, Baka living in communities closer to the market town purchase all of their sweets from the market (e.g., candy), while people living in more isolated villages gather all of their sweets from the wild (i.e., honey; Reyes-García et al., 2019).

Given the Baka's reliance on a mix of forest resources, crops, and purchased foods, the Baka represent an ideal group to explore the activity costs compared between gathering and other subsistence activities, such as hunting, farming, and fishing, and further to investigate how gathering costs might vary among different food items. Based on what has been previously published about the division of labor by age and gender among Central African hunter-gatherer groups (Hewlett, 2014), and our own previous experiences among the Baka, we are able to make several hypotheses about patterns of subsistence activities among the Baka. First, we expect Baka women to engage more in gathering activities than men, and that involvement in foraging activities will decrease with age. In line with the grandmother theory and cultural transmission (Hewlett, 2014), we expect elders to devote more time in activities different from food acquisition such as child care taking, resting or socializing. We also expect that the intensity of work will differ among activities given that they require different techniques and levels of physical engagement (e.g., Gurven et al., 2013; Meehan et al., 2013). Furthermore, we expect that this intensity should decrease with age, as physical strength often decreases after about 45 years old (as summarized in Walker et al., 2002), and roles and activities within the community change. In addition, we expect that the duration and distance traveled will also vary among activities, given that resources are located in different areas. In particular, we anticipate that hunting will require greater travel distances and more time than other subsistence activities (Wood et al., 2021). Because each settlement is located in a specific ecological landscape, with different distances to fields, hunting grounds, and other resources, we also anticipate that the kind of settlement would influence the duration of particular activities, such as crop harvesting. We also expect that individuals from settlements with higher market integration, for example, located closer to a market town and to the Bantu villages, would engage more in wage labor and other non-subsistence activities, and less in foraging activities, especially in gathering wild plants, than more isolated settlements such as forest camps. Finally, we expect a large variation in intensity of work, duration, and distance traveled within "gathering" activities given the diversity of products gathered and the different techniques needed to access them (Gallois et al., 2020).

METHODOLOGICAL APPROACH

This study took place in four Baka settlements in the Lomie and Messok district of the Haut Nyong division in southeastern Cameroon. The primary Bantu-speaking group in this region is the Nzime. Because the availability of food and the time allocation of the Baka vary considerably throughout the year, the data were collected during three fieldwork periods of 7 weeks during three different seasons: the major dry season (January–February 2018), the major rainy season (October–November 2018), and the minor rainy season (April–May 2019).

Before the onset of the study, we obtained Free Prior and Informed Consent (FPIC) from every individual taking part in this research. This study adhered to the Code of Ethics of the International Society of Ethnobiology, and received the approval of both the ethics committee of Leipzig University (196-16/ek) and the Ethical Committee from the Ministry of Health of Cameroon (n°2018/06/1049/CE/CNERSH/SP). All data were collected within the context of immersion into Baka life, with the first author living directly in the settlements and participating in domestic work. The interviews were conducted directly by the first author who had previously learned the Baka language and with the help of a local research assistant who spoke the Baka language.

Data Collection

In the four studied villages, we collected socio-demographic data at the individual level regarding the gender and age of the participant, and established the kinship chart among all participants in each village. As the Baka do not have any birth records, we estimated their age by using kinship information and the previously established estimates for age of first birth (18 years old) and birth interval (2.5 years old) (Ramirez Rozzi et al., 2015). We also estimated the level of market integration of the settlement by collecting data on the number of inhabitants, the proximity to the market town, and the presence of shops, schools, and health services (**Table 1**).

We assessed how the Baka spent their time and energy while performing subsistence activities by combining GPS (Global Positioning System) and heart rate records during their daily activities with self-reported time allocation recalls. Specifically, we invited the participants to wear an activity monitor that included a GPS device and a chest-worn heart rate monitor (Garmin fēnix® 3/HR) during their daily tasks. They were asked to wear the activity monitor during the whole active period, from early in the morning (between 6 a.m. and 8 a.m.) to the end of their day, when they were back in the village and had ended their activities (between 5 p.m. and 7 p.m.). In addition to these records, we interviewed each participant when they returned the activity monitors, asking them to report all of the activities they had performed and the products they had gathered while wearing the GPS device (time allocation recall). We also calculated an approximate duration of the activities using mostly solar references, which has been recently shown to be a good predictor for hunter-gatherers living in rainforest environments (Jang et al., 2019). We included all individuals willing to participate in this study with the aim of getting a sample that was balanced in terms of age categories and genders. A total of 246 daily GPS tracks and heart rate records were collected (156 among women, 90 among men) among 153 individuals (97 women, 56 men). Seventy-nine individuals were interviewed once, 55 twice, and 19 three times (**Supplementary Material 1**).

We also collected contextual information related to how the Baka spent their time on subsistence tasks and additional ethnographic data by conducting informal interviews with men and women separately in order to ensure both genders were equally heard. We asked questions about perceived effort (e.g., "what is the most difficult activity that you do?"), seasonal calendar, group composition (e.g., "with whom do you usually perform [subsistence activity]?"), food sharing practices, and other aspects of their livelihood. Moreover, the previous long period of fieldwork spent by the first author – more than 30 months in total – living directly in Baka settlements provided us additional information that has been used for further contextualizing our results.

Variable Constructions

We first extracted the data from the activity monitor, namely the GPS position, the heart rate, the speed, and time. These data were recorded every second throughout the day, and data for each second is called an epoch. Commercial activity monitors such as we used are known for occasionally recording epochs with biologically unrealistic speeds (<0 or >8 m/s) (Pontzer, 2015) and missing or unrealistic heart-rate values ($>208-0.7 \times \text{age}$) (Tanaka et al., 2001). We cleaned the data to remove these errors by removing these epochs from the daily record. After cleaning, the records were on average 38,056 s long (about 10 h 34 min). Combining the self-reported time allocations and the tracks recovered from the GPS locations, we identified on the individual daily records: (a) the time spent outside and inside the settlement, and (b) the different activities performed. We also calculated the duration, distance traveled, and energy expenditure for both the actual performance of the activities. Each activity record included the travel to reach and leave from the place where the activity took place (for example, the travel to the forest spot, the actual moment of hunting, and the travel back to their settlement).

For assessing energy expenditure while performing their daily activities, we used the formulae proposed by Keytel et al. (2007), which provide an estimate of energy in kJ per minute based on heart rate in beats per minute. For men, this formula was: $-55.0969 + 0.6309 \times$ Heart rate (in beats per minutes) $+ 0.1988 \times$ Weight (in kg) $+ 0.2017 \times$ Age (in years); and for women: $-20.4022 + 0.4472 \times$ Heart rate $+ 0.1263 \times$ Weight $+ 0.074 \times$ Age. Every second, the activity monitor estimated the average heart rate in beats per minute. We applied these formulae to calculate energy expenditure from heart rate value every epoch. This provided estimates of energy

TABLE 1 | Description of the four Baka settlements included in this study.

Settlements	Type of settlement	Approximate number of inhabitants	Proximity to the market town (km)	Number of shops	Schools and health services	Other relevant characteristics
Le Bosquet	Village along logging road	800	26	4	1 private school and health center (missionaries)	Big settlement built by missionaries and long visited by foreigners (missionaries and researchers).
Mombokola	Village along logging road	500	12	3 (in the Nzime village)	1 public school – no health service	At the crossing of several logging roads. Base of one logging company. In continuation of the Nzime village.
Elonda	Village along logging road	400	33	1	1 private school – no health service	2 km from the Nzime village.
Kungu	Forest camp	200	11 (including 4 km in the forest, 1.5 h of walking)	0	1 public school in the Nzime village (1.5 h away) – no health service	Settlement in the forest where people live occasionally. Residents of the forest camp also have a house in a village along the logging road that is a continuation of a Nzime village, about 1.5 h walk away.

consumption in kJ per minute for each epoch, so we therefore divided this value by 60 to have the energy expenditure in kJ per second for each epoch. We summed these kJ per second values over the entire set of seconds in order to obtain the total energy expenditure for each activity.

For the resting basal metabolic rate (BMR), we used the New Oxford formulae proposed by Henry (2005), which account for variation in BMR due to weight, gender, and age. These were: for men between 18 and 30 years-old: 0.0669 × Weight (in kg) + 2.28; men between 30 and 60 years-old: 0.0592 × Weight + 2.48; men 60 + years old: 0.0563 × Weight + 2.15; For women between 18 and 30 years old: 0.0546 × Weight + 2.33; women between 30 and 60 years old: 0.0407 × Weight + 2.90; women 60 + years old: 0.0424 × Weight + 2.38. In all cases, these formulae provide BMR in MJ per day, so we then converted the resulting values to kJ per minute.

For every self-reported activity, we calculated the metabolic equivalent of task (hereafter, MET) following Ainsworth et al. (2011) as the ratio of the average energy expenditure spent in kJ/min during each activity to the average energy expenditure spent in kJ/min by that individual when resting. Using MET instead of summed kJ spent per activity allows us to account for differences in BMR among individuals. It also averages out potentially unrealistically high or low energy values (in kJ/min) that might be the result of errors in the measurements taken by the activity monitors. While we were not able to directly assess unrealistically high or low energy values, we did explore the potential variation in heart rate values within and among a subsample of the recorded activities (**Supplementary Material 2**) in order to assess if the MET values provide a realistic estimate of the overall intensity of the task. With the exception of water carrying, which demonstrated a pattern of low or/moderate heart rate followed by high heart rate values, there were no distinct patterns of heart rates among activities. Within each activity, some individuals had a moderate and steady heart rate throughout the activity, while others showed a lower heart rate with punctuated episodes of higher heart rate. Overall, MET values appear to accurately reflect the average intensity of a task. A final advantage of using MET is that it provides a unit-less indication of the effort put into an individual task, or, in other words, the intensity of the work.

We then used these data in a number of different analyses to investigate: (1) daily time allocation, (2) duration, distance traveled, and intensity of work among the different activities, and (3) detailed exploration of gathering activities. We specifically compare between genders (men and women), among villages, and among age categories. We chose the four villages explicitly given their different levels of market integration, distance to market towns, distance to agricultural plots and proximity to Nzime villages. We divided the participants into three age categories: under 30, 30–60, and older than 60. Hunter-gatherers reach their highest foraging productivity at 30 years old (Koster et al., 2020), so we used this age as the division between young and middle-aged individuals, while 60 is considered the start of senior years in many demographic studies.

Data Analysis

Daily Time Allocation

First, we explored how the Baka spent their time among various subsistence activities. In each daily record, we calculated the percentage of time that the Baka spent outside the settlement. We then compared the time spent outside the village among villages, between genders, and among age categories. As we were primarily interested in food acquisition activities, we then focused on those that took place outside of the camp. We classified each self-reported activity into one of eight different categories: (1) gathering, (2) hunting, (3) fishing, (4) agricultural work (e.g., field maintenance, weeding, etc.), (5) crop harvesting (e.g., acquisition of food items for consumption or sale), (6) firewood collection, (7) water fetching, and (8) others. This latter category includes the following activities: gathering building material, logging, other wage jobs, traveling to other villages, and visiting other villages. We observed 531 activities. If one individual reported that they performed the same activity on separate trips in the same daily records, we counted this as one observation in order to avoid inflated data per activity, which reduced the total analyzed activities to 513. We compared how the participation in the various activities varied between genders, across age categories and among villages.

Energy Spent on Activities

Second, we explored the effort spent by the Baka among activities. We measured effort by looking at the duration, the distance traveled, and the MET across activities, and explored whether these varied between genders, among villages and among age categories. For these analyses we had to use a reduced dataset that included only those records in which a single activity was reported. As we discuss in detail below, many of our participants reported performing multiple activities in the same trip outside the settlement (e.g., crop harvesting and fuel collecting). We could not separate the time and energy spent on these activities in our records. Therefore, our reduced dataset included only 258 activities, from 202 individual daily records in which the participant reported performing "single" activities. We first examined the relationship between distance and duration by performing two power correlation tests. Based on the results (in detail below) we opted to proceed further with only the duration of the activities. We specifically predicted that the intensity of effort (as measured by MET), and the duration of the task (time in minutes) should vary among activities between men and women (e.g., women spend effort and/or more time on gathering than do men). We also predicted that the work might vary among activities between villages (individuals in forest camp might spend more effort and/or more time on gathering than those in Le Bosquet). Finally, we predicted that the energy spent should vary among activities between age categories (older individuals might spend less effort and/or time on gathering).

These predictions led to us building two general linear mixed models (GLMMs) which tested the effects of these interactions, one on duration of the activity, and the other on MET as a measure of intensity of effort. In both models, activity, age, gender, and village were included as fixed effects, with interactions between gender and activity, age category and activity, and village and activity. Because we were explicitly testing the effect of the interactions of activity and the other factors, we had to remove activities that were incompletely nested. In our observations, only women went fishing, so we removed this activity from the data set. Furthermore, we did not observe water carrying among individuals in our oldest age category. We therefore also removed this activity from the data set. Finally, because the "other" category included a variety of different activities, we would not expect a coherent pattern in either the duration or the intensity for this activity. We therefore removed it from the data set. This left us with a dataset of 216 observations of five activities (gathering, crop harvesting, hunting, firewood collection, and agricultural work).

Given that we observed some of the same individuals multiple times, and that our observations were spread out over several different days, we included the subject number and date of observation as random effects. Furthermore, we noted that different activity monitors could provide differing but internally consistent measurements, so we also included the number of the activity monitor as a random effect.

Prior to running the analyses, we log transformed and then z-transformed to a mean of zero and standard deviation of one both duration and MET values in order to improve model fitting. The models were fitted using the function lmer of the R package lme4 (Bates et al., 2015), with a Gaussian error distribution and identity link function, using maximum likelihood (REML = FALSE) to make it possible to compare among models with different random effects structures.

As a last exploration of energy expenditure, we estimated the total energy spent on the various activities across all of the records in our single-activity data set. Given the potentially unrealistically high values recorded by the activity monitors, we chose not to use the total kJ values. Instead, we multiplied the MET value (average intensity) by the duration of the activity per record. We then averaged this calculated energy value across all observations of the activity, then multiplied this average MET by the frequency of occurrence of that activity to get a sense of the energy budget per activity and per activity between genders.

Gathering

Third, we more closely explored gathering activities themselves, with the goal to see if gathering varied among the different wild products that were collected. From the 106 gathering events recorded, we could extract the duration and MET values for 51 gathering activities: 36 among women and 15 among men. We then compared the duration, distance traveled, and MET among the different wild foods that were collected. We finally estimated the total energy spent while gathering the various food items as a proportion of the total energy budget, by multiplying the average MET by the average duration per food item, and then multiplying this by the frequency of gathering that food item within the total number of activities.

Our data were analyzed using a combination of Stata 11.1 and R version 3.6.3 (2020-02-29) – "Holding the Windsock" (R Core Team, 2020).

Limitations

We recognize that there may be inaccuracies in the self-reporting and the data provided by the activity monitors. However, we chose to use interviews and activity monitors instead of other methods for assessing energy expenditure such as focal follows and oxygen monitors, because these allowed us to maximize the number of participants and to interfere the least with their habitual behaviors. We were also interested in separating out daily activities, so methods such as doubly labeled water were not appropriate for this analysis. A further caveat is that the "MET" value for each activity that we derived from calculations based on heart rates does not necessarily match those published elsewhere (Ainsworth et al., 2011) and may therefore not be broadly applicable for comparisons of activities beyond the scope of this article. However, as the aim of this research is to compare the effort between the different activities within a single community and using one method set, by standardizing our activities by the individual's BMR, we can compare the MET between the different activities and individuals.

RESULTS

Daily Time Allocation

Outside the Settlement

The Baka regularly leave the settlement: Of the 246 individual daily records, only 17 recorded staying in the settlement the entire day either for performing activities such as house maintenance, handicraft, socializing, or for resting. Overall, individuals traveled an average of 15 km (SD = 5.2), with no significant difference between men and women (men: 16.1 km ± 6.4; women: 14.8 km ± 4.3; Wilcoxon signed rank tests: $z = -1.44$, $p = 0.15$). Individuals who left the settlement spent an average of 260 min, or 4 h 20 min, away (SD = 164 min). Compared to the total time recorded, about 39% of the day was spent outside of the settlement.

Plotting the percentage of time spent outside revealed interesting patterns (**Figure 1**). While there was no difference between men and women, we did observe differences among age categories: individuals above 60 years old spent less time outside of the settlements than the other two age categories. The amount of time spent outside also varied among settlements, with individuals living in Le Bosquet and Mombokola – the two larger settlements – spending less of their time outside than those in Elonda and Kungu.

Involvement in Food Acquisition Activities

While away from settlement, the Baka reported a total of 531 different activities that they conducted in 419 different trips. Note that here we distinguish between a trip outside the village and a daily record – in 1 day an individual might make one or more trips. In some cases, the Baka performed multiple activities in the same trip, for example, leaving the settlement to work in the agricultural plots, and also gathering wild plants and collecting firewood at the plot or along the way. We found that 49% of the activities ($n = 207$) were reported as combined activities, meaning

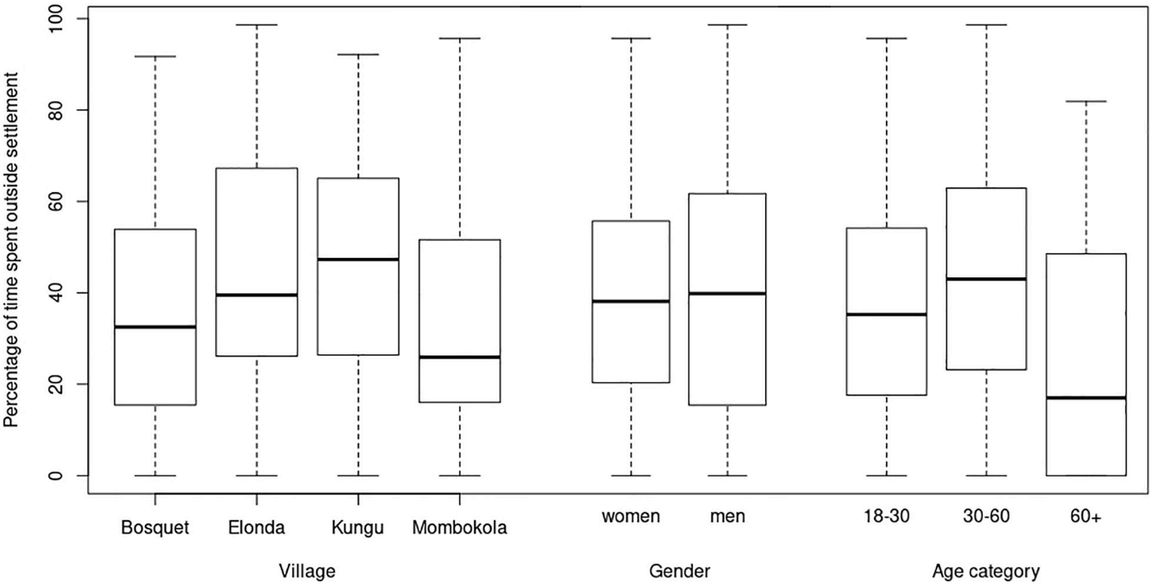

FIGURE 1 | Percentage of time spent outside of the settlement across all daily records, shown separated by village, by gender, and by age category. The central line indicates the median and the boxes cover the interquartile range. The whiskers indicate the entire range.

that the participants left the settlement and conducted different activities in a single trip before going back to the settlement.

On average, the Baka engaged most frequently in agricultural work (51.2% of the out of the camp activities), and gathering (41.1%), followed by crop harvesting (29.7%), and firewood collecting (27.6%). In contrast, hunting and fishing were the least frequently performed (14.6 and 4.5%, respectively) (**Figure 2**). Men and women engage differently in their daily activities outside of the settlement. Women tend to engage more frequently than men in crop harvesting, firewood collecting, fishing, and water fetching. Men are more frequently involved in hunting than women (**Figure 2**).

The occurrence of the different activities also varies among age categories and villages. The youngest individuals more frequently conducted water fetching and fishing than the two older age categories. Individuals in the middle age category more frequently engaged in agriculture than both other age categories (**Figure 2**). Inhabitants of Elonda, a village of about 400 individuals settled along the logging road, reported less gathering than the others. Individuals from both Elonda and Mombokola reported agricultural work and crop harvesting more frequently, but fishing less often than in both other villages (Kungu and Le Bosquet). Individuals from Kungu, the forest camp, performed hunting more frequently than those in all other settlements (**Figure 2**).

Duration, Distance, and Metabolic Equivalent of Task of the Food Acquisition Activities

Duration and Distance Traveled

Among the reduced data set of "single" activities, there was significant variation in the duration of the activities, from 45 min to more than 5 h (Kruskal–Wallis test: $X^2 = 100.46$, $p = 0.0001$) and distance traveled from 1.61 to 17.23 km ($X^2 = 96.86$, $p = 0.0001$). Specifically, fishing and hunting required more time and the furthest travel (**Table 2**). In contrast, gathering did not require a similar investment in travel (7.7 km, 169 min), and the shortest distances were traveled while collecting firewood and fetching water (**Table 2** and **Figure 3** for the distance where took place the main activities, by settlement).

Distance and duration were correlated, according to the results of two series of power correlation tests ($p < 0.000$), one taking all recorded activities together (Pearson's correlation coefficient = 0.923) and the other by category of activities (coefficients = gathering: 0.97; hunting: 0.961; fishing: 0.985; agriculture: 0.906; crop harvesting: 0.958; water fetching: coef = 0.878; fire collecting: 0.879; and others: 0.958). Therefore, to simplify our results, we used only the duration of the activities in our further analyses.

In the GLMM exploring the influence of our main factors and their interaction on the duration of the activities, we discovered that the full model with all three random effects (subject number, date, and activity monitor number) provided a singular fit. Given that date and activity monitor number had no effect on the MET (see below), and that we anticipated that these potential influences should have even less effect on duration than on MET, we therefore retained only subject ID as the random effect in our further analysis. We checked whether the assumptions of normally distributed and homogeneous residuals were fulfilled by visually inspecting a qqplot and the residuals plotted against fitted values. Both indicated no obvious deviations from these assumptions. We checked for model stability by excluding data points one by one from the data and comparing the estimates and fitted values derived with those obtained from the model based on all data. These indicated some potentially influential

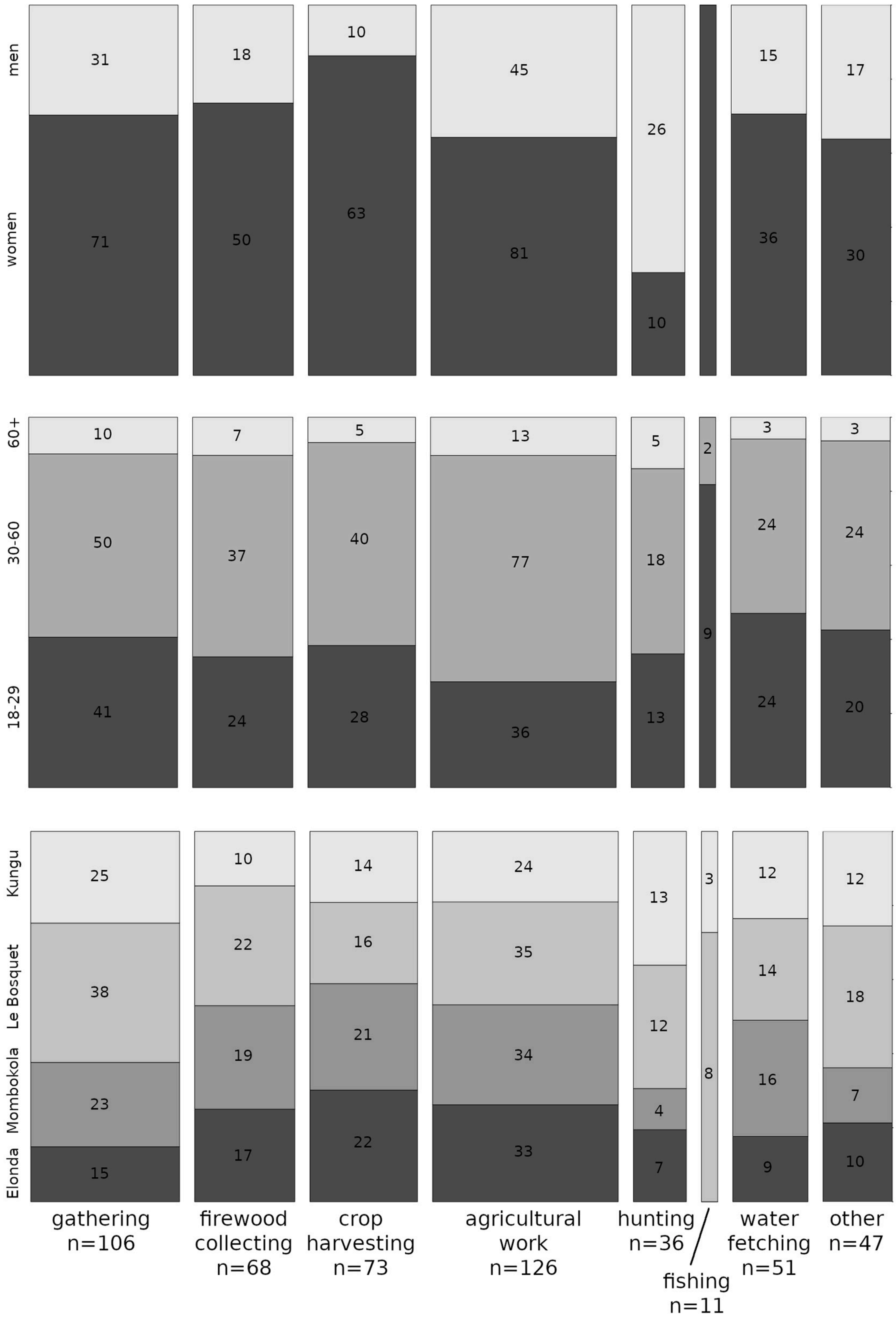

FIGURE 2 | Occurrence of the activities, shown separated by gender, age categories, and villages.

TABLE 2 | Average MET, time spent, and distance traveled among subsistence activities observed in 202 records from 135 individuals (90 women and 45 men).

	Recorded single activities			MET						Duration (in minutes)						Distance in km					
				Total		Women		Men		Total		Women		Men		Total		Women		Men	
	Total	Women	Men	Average	SD	Average	SD	Average	SD	Average	SD	Average	SD	Average	SD	Average	SD	Average	SD	Average	SD
Crop harvesting	28	26	2	8.26	1.82	8.30	1.89	7.82	0.69	121.76	144.26	121.80	149.53	121.25	54.08	4.91	6.60	4.93	6.83	4.6	3.11
Water fetching	22	15	7	7.28	1.68	7.99	1.45	5.75	0.83	37.70	20.73	37.39	18.26	38.36	26.94	1.82	0.97	1.81	1.00	1.85	0.99
Firewood collecting	27	22	5	6.94	1.74	7.15	1.41	5.98	2.80	45.35	24.01	44.03	23.43	51.12	28.57	1.61	1.02	1.55	0.89	1.90	1.56
Agricultural work	94	61	33	6.92	2.17	6.86	2.01	7.06	2.48	232.05	134.41	228.32	131.35	238.95	141.72	8.15	4.90	7.71	4.28	8.96	5.86
Gathering	51	36	15	6.82	2.76	7.11	2.89	6.14	2.38	169.32	143.54	146.39	123.07	224.35	176.41	7.7	7.27	6.49	5.84	10.61	9.51
Others	13	9		6.66	2.62	6.44	1.95	7.17	4.1	192.23	158.77	153.0	152.5	280.49	232.89	9.18	8.64	6.09	5.73	16.15	16.36
Fishing	7	7	0	6.4	1.37	6.4	1.37			334.34	172.17	334.34	172.17			17.23	8.54	17.23	8.54		
Hunting	16	4	12	6.33	2.43	7.74	1.58	5.86	2.53	239.72	153.04	91.99	35.70	291.18	141.54	11.74	8.47	3.63	1.63	15.45	8.07
Snares	3	1	2	6.98	2.27	8.97		5.98	2.08	276.56	148.76	123		353.33	94.28	15.73	11.24	5.4		20.9	9.62
Unearthing	6	1	5	5.53	2.54	7.04		5.23	2.72	278.96	187.83	50.02		324.75	168.45	12.52	9.34	2.1		14.6	8.74
Other (spear, shotguns)	7	2	5	6.74	2.56	7.47	2.31	6.44	2.85	190.3	129.27	84.13	33.99	232.76	129.96	9.37	7.02	3.5	1.56	11.72	7.01

cases. Examination of the data revealed that in the 60+ age category, there were only two individuals who collected firewood, only two who harvested crops, and only two who hunted. We chose not to exclude any of these cases from the model because doing so would have resulted in an incompletely nested structure. Variance Inflation Factors (ViF) were derived using the function vif of the package car (Fox and Weisberg, 2011) applied to a linear model excluding the random effects. These values were all below 2.5 suggesting no problems. The full model was significant as compared to the null model which comprised only subject ID as the random effect (likelihood ratio test using the ANOVA function with the test set to "Chisq" $\chi^2 = 123.21$, df = 34, $p < 0.001$). *p*-Values for the fixed effects and interactions were based on the function ANOVA of the package lmerTest (type II analysis of variance with Satterthwaite's method, Kuznetsova et al., 2017).

As we expected, the amount of time spent varied significantly among the activities. Crucially, the amount of time spent on a task was significantly influenced by the interaction of activity and village, with individuals in le Bosquet spending significantly less time on both crop harvesting (df = 196.90918, $t = -4.098$, $p < 0.001$) and on agriculture (df = 202.15752, $t = -3.129$, $p = 0.002$) than any other activity and village combination (**Figure 4** and **Supplementary Material 3**).

Metabolic Equivalent of Task

Metabolic equivalent of task values allowed us to compare the average cost of individual activities regardless of the time spent. We first explored whether MET values correlate with duration and distance, both considering all activities together or individually. Pairwise correlation tests showed no correlation between duration and MET (coefficient = −0.0651, $p = 0.30$) or between distance and MET (coefficient = −0.0239, $p = 0.702$). We explore whether the average MET values varied according to the activity performed, the gender, the age category, and the village of the informants (**Table 2**). The most energy demanding activities are crop harvesting (8.26), water fetching (7.28), and agricultural work (6.94). Interestingly, the MET of gathering – 6.82 – is higher than those of fishing (6.4) and hunting (6.33) (**Table 2**).

For the GLMM in which we tested whether MET was significantly influenced by activity, age, gender, village, and the interactions among age and activity, gender and activity, and village and activity, we first tested whether our random effects (subject ID, date, and activity monitor number) significantly improved the model fit. We therefore removed each one individually and compared to the full model. These tests indicated that the model that removed the date did not significantly differ from the full model (likelihood ratio test using the ANOVA function with the test set to "Chisq": $\chi^2 = 0.9144$, df = 1, $p = 0.339$). The model that removed the activity monitor number also did not significantly differ from the full model ($\chi^2 = 0.2104$, df = 1, $p = 0.646$). We therefore removed both of the random effects from further analyses. However, removing the random effect of the subject number was highly significant, ($\chi^2 = 21.324$, df = 1, $p < 0.001$) so we retained this in our further analysis. All tests for model assumptions, model stability and ViF were completed as described above. As above there were indications

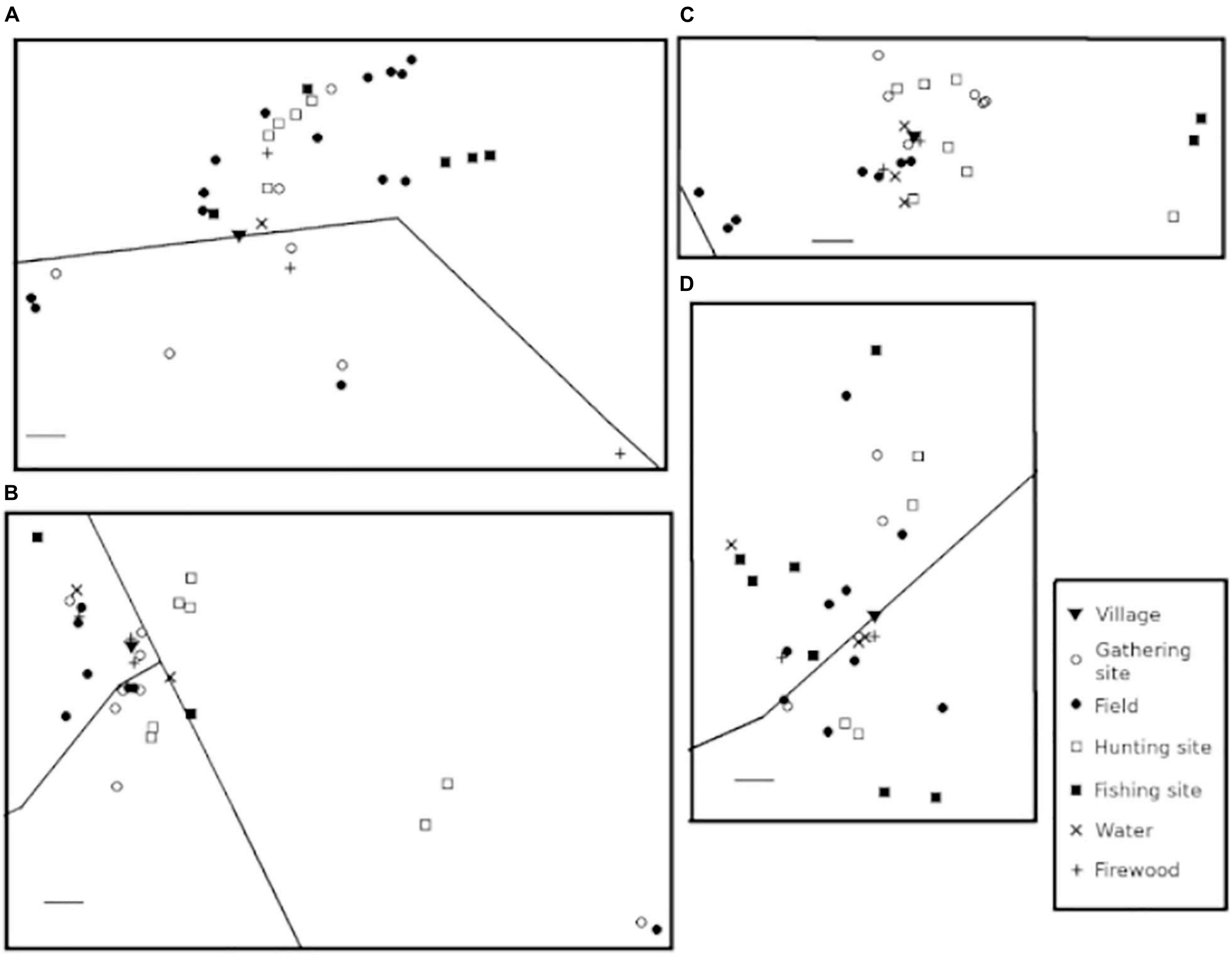

FIGURE 3 | Schematic representation of the villages, indicating the locations of the different activities (**A**, Le Bosquet; **B**, Mombokola; **C**, Kungu; and **D**, Elonda). The straight lines through the images represent roads. The scale bar in the lower left of each sub-image represents 500 m.

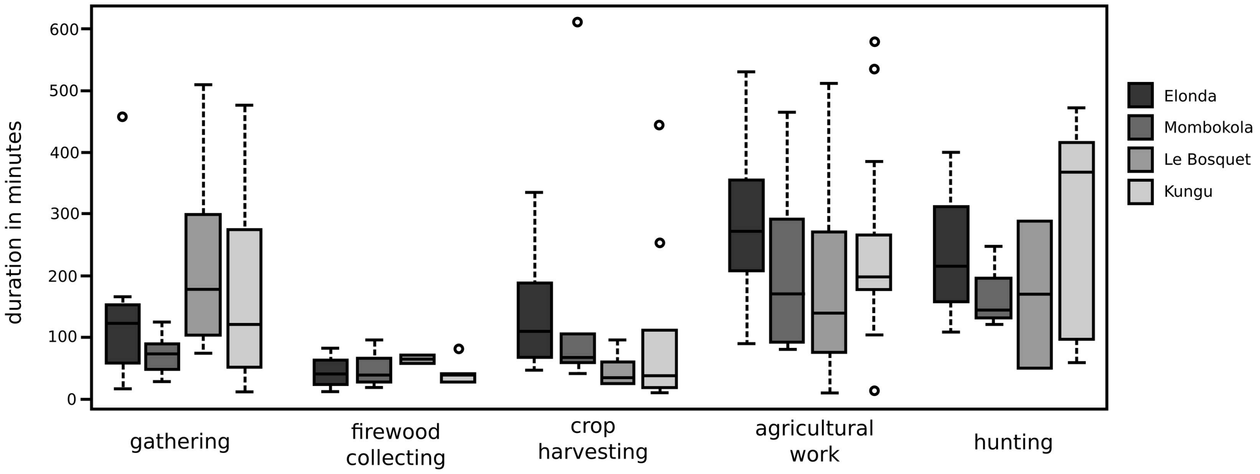

FIGURE 4 | Time spent during the activities, by village of the informants. The central line indicates the median and the boxes cover the interquartile range. The whiskers indicate the entire range.

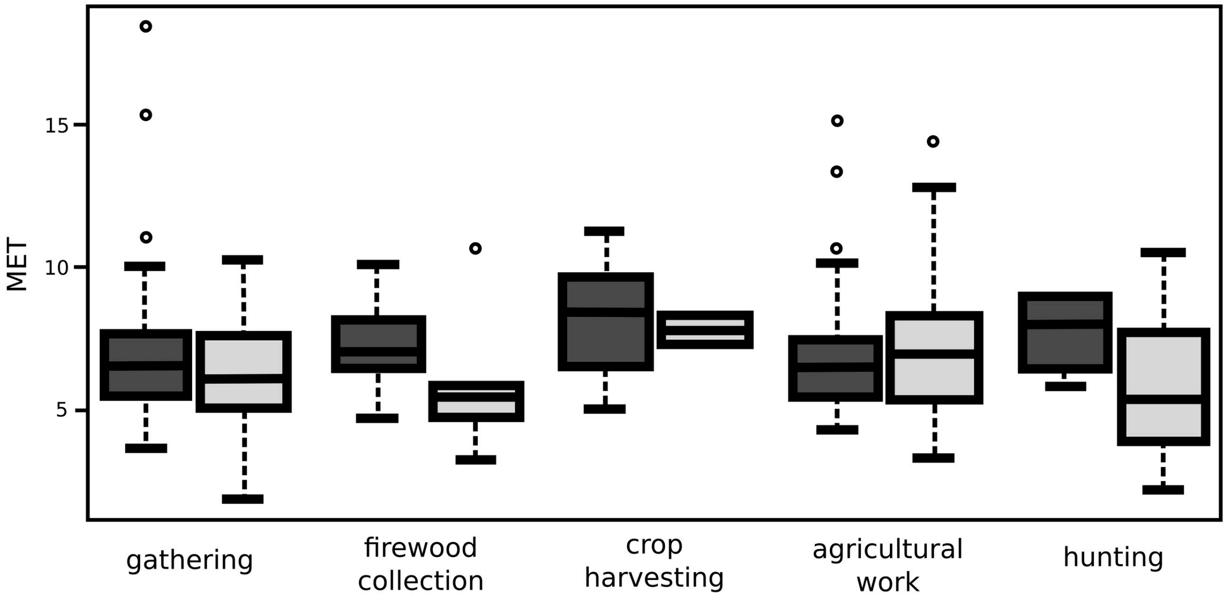

FIGURE 5 | Metabolic equivalent of task of the different activities, by gender. The dark color indicates records for women, and the lighter color for males.

for influential cases in the 60+ age category due to a limited number of records, but we chose not to exclude these. The other tests revealed no other significant problems. The significance of the full model as compared to the null model (comprising only the random effect) was established using a likelihood ratio test ($\chi^2 = 60.26$, df = 34, $p = 0.004$). *p*-Values for the fixed effects and interactions were based on the function ANOVA of the package lmerTest.

All of our individual predictors were combined in interactions, therefore we cannot individually assess their effect on the model. Of the three interactions, only the interaction of activity and gender was significant (df = 4, dendf = 173.10, $F = 4.7841$, $p = 0.001$). Men had significantly higher MET values than women when performing agricultural tasks (df = 163.765183, $t = 3.320$, $p = 0.001$). Men also showed slightly lower MET values for hunting, but this was not significant. The model also revealed that while age and gender overall might have an influence on intensity as measured by MET, these effects did not differ among activities (in other words, the interaction was insignificant) (**Figure 5** and **Supplementary Material 3**).

Finally, we aimed to get an overall descriptive overview of the total amount of energy dedicated to each of the activities within our data set, we multiplied the average MET per activity by the average duration, and then multiplied this by the frequency of that activity within our dataset. Given their high MET values, moderate duration times, and high frequency of occurrence, agricultural work and gathering are the two most energetically expensive activities, and constitute respectively about 36 and about 20% of the total energy spent outside the settlement for the whole sample, and for women respectively 39 and 20% and for men 34 and 23% (**Table 3**). The next most costly activities varied between the genders, with women spending about 19% of their energy in crop harvesting, while men engage a similar amount of energy in hunting, and also in performing activities outside the settlement other than for food acquisition, as for instance cutting and collecting wood for house building or visiting other villages for social reasons.

Detailed Exploration of Gathering Activities

To assess how the costs of gathering can vary across food items, we compared the characteristics (MET, duration, and distance) of gathering among individual wild products.

Of the 51 gathering events analyzed, most of them were for gathering **koko** leaves (*Gnetum africanum*). There were in total 27 **koko**-gathering trips, including three events during which other wild edibles were also collected (in the "Various" category, **Table 4**). The second most frequently gathered products were the tubers of wild yams (*Dioscorea* spp.), conducted in eight records, including two trips during which other wild edibles were collected. Both men and women gather leaves, mushrooms, and yams, but only men gather honey and cut palm trees for gathering their sap and making palm wine. In our sample, only women gathered the fatty fruits from *Elaeis guineensis*, but this might be due to the small number of records, as both men and women reported to us that men regularly engage in gathering these fruits.

While all of these activities fall under the general heading "gathering," there are considerable differences in the distance traveled and time spent for acquiring each food type (**Table 4**). Honey gathering requires the furthest distance. Gathering trips targeting more than one product require considerable distance to cover, as does collecting yams (**Table 4**). In contrast, palm wine gathering takes the shortest distance traveled, because the palms are usually close to the settlement or to their fields.

TABLE 3 | Amount of energy dedicated to each of the activities, estimated by multiplying the average energy spent in the activity by the average duration of the activity, and then by the frequency of occurrence of the activity across all of the daily records (258 activities from 202 individual daily records).

Activities	Whole sample				Women				Men			
	Number of records	Total energy estimated	SD	Relative proportion	Number of records	Total energy estimated	SD	Relative proportion	Number of records	Total energy estimated	SD	Relative proportion
Agricultural work	94	802.79	538.67	0.36	61	767.47	473.78	0.39	33	868.08	644.7	0.34
Gathering	51	447.11	431.03	0.20	36	392.54	312.64	0.20	15	578.07	626.99	0.23
Fire collecting	27	85.98	53.82	0.04	22	88.38	57.69	0.04	5	75.4	34.42	0.03
Crop harvesting	28	304.68	408.37	0.14	26	306.06	423.3	0.15	2	286.81	150.21	0.11
Hunting	16	199.12	141.34	0.09	4	95.42	44.98	0.05	12	233.68	146.54	0.09
Fishing	7	91.03	51.97	0.04	7	91.03	51.97	0.05	0			0.00
Water fetching	22	57.42	34.69	0.03	15	63.35	35.47	0.03	7	44.73	31.63	0.02
Others	13	267.4	309.32	0.12	9	178.89	190.49	0.09	4	466.57	547.76	0.18
Total	258	2255.53		1.00	180	1983.14		1.00	78	2553.34		1.00

Similarly, the intensity of work needed during collecting these different foods varied (**Table 4**). The MET values of gathering varied the most among all of other subsistence activities (SD = 2.76; **Table 2**), suggesting that this category in fact subsumes a wide number of tasks that differ energetically. While the leaves of *G. africanum* are the most frequently gathered product, they require the lowest intensity. The gathering of the oil-rich nuts and seeds, including **kana** (*Panda oleosa)*, **bokoko** (*Klainedoxa trillesii*), **mbila** (*E. guineensis*), and **payo** (*Irvingia spp.*) requires the greatest intensity. These nuts often have very thick shells, so the Baka crack the shell to open the fruits and gather the seeds (except for *E. guineensis*). The gathering of yams is also high intensity work, because they grow quite deep in the ground, up to 3 m deep (Dounias, 2001) and the Baka have to dig them up. This activity is more energetically demanding than honey gathering, partly because during our field seasons the Baka collected only the honey of bees who nest in fallen trees.

When considering the products individually, it is noteworthy that the MET of gathering nuts is higher than that of crop harvesting (9.52 vs. 8.26, respectively). Likewise, the gathering of yams and of honey have MET values just between those of crop harvesting and water fetching. The collection of these products is therefore among the most energy demanding subsistence activities performed by the Baka. Finally, regarding the amount of energy dedicated to each of the gathering activities we see the gathering of koko leaves and various wild edibles were the two most energetically expensive gathering activities, and constitute respectively about 36 and about 24% of the total energy spent for gathering for the whole sample, and for women respectively 43 and 24% and for men 31 and 39% (**Table 5**).

DISCUSSION

Food Acquisition Activities in a Mixed Subsistence Society

Our data reveal that agricultural tasks (including working in the field and harvesting crops), are the main activities undertaken by the Baka on a daily basis, followed by gathering wild resources. This first overview confirms that the Baka from this area in southeastern Cameroon rely on a farming-foraging livelihood, not only hunting and gathering. Agriculture is highly valued (Gallois, 2017), and the Baka tend to prefer domesticated crops above most other foods (Gallois et al., 2020). These preferences may be due in part to: (1) multiple and ongoing political and developmental campaigns that promote agriculture in Cameroon, (2) perceptions of a higher social status that may be associated with having agricultural fields (Gallois, 2017), or (3) personal taste preferences for crop foods. The way the Baka engage in their subsistence activities is not homogenous in the studied area, with slight differences among the settlements. While people from the forest camp tend to conduct hunting more frequently than in the other settlements, gathering was reported more frequently in a village settled along the logging road (Elonda). Baka living in the forest camp were not isolated from agriculture or from wage labor opportunities, likely because this forest camp was quite close to the village (about 1.5 h walking), which made it possible to travel there and back from the closest Nzime village within 1 day. Furthermore, variability exists between the villages settled along the logging road, likely due to their individual social and ecological contexts. Elonda and Mombokola seemed to be more orientated toward agriculture than Le Bosquet, for which the frequency and duration of agricultural tasks were lower than both other settlements. Mombokola and Elonda are closer to Nzime villages than is Le Bosquet, which might increase the frequency and duration devoted to agriculture because the Baka more frequently engage in wage labor by working in Nzime fields. Inhabitants of the two largest villages (Le Bosquet and Mombokola), spent less time outside the settlement, possibly due to more opportunities for subsistence activities within the settlement (e.g., selling products and wage labor). To further develop our understanding of drivers of time allocation, future work is needed to better quantify the different social, ecological, and economic factors of each village, but equally as importantly, to explore the factors affecting household and individual decisions of time allocation.

As has been previously seen in other studies, our data also showed that both women and men tend to engage in similar activities. Even if fishing and hunting are more frequently performed by one gender, there is not any apparent restriction

TABLE 4 | Metabolic equivalent of task, duration, and distance traveled in gathering activities, by wild edible products; for the whole sample and by gender.

	Number of records			MET						Duration in minutes						Distance in km					
				Total		Women		Men		Total		Women		Men		Total		Women		Men	
Wild edibles	**Total**	**Women**	**Men**	**Average**	**SD**	**Average**	**SD**	**Average**	**SD**	**Average**	**SD**	**Average**	**SD**	**Average**	**SD**	**Average**	**SD**	**Average**	**SD**	**Average**	**SD**
Nuts	5	4	1	9.52	5.09	10.46	5.36	5.76		116.07	90.67	114.58	104.63	122.02		6.9	4.65	7.23	5.31	5.6	
Yams	6	5	1	8.21	4.83	9.47	4.15	1.89		239.14	196.07	231.92	218.32	275.28		11	9.93	10.62	11.05	12.9	
Honey	4	0	4	8.08	2.10			8.08	2.10	417.48	97.45			417.48		21.78	3.95			21.78	3.95
Mushrooms	5	3	2	7.15	0.98	7.08	0.82	7.24	1.58	100.03	100.94	126.42	128.89	60.43	47.99	4.38	4.85	5.9	6.12	2.1	1.41
Palm wine	2	0	2	7.15	2.29			7.15	2.29	46.49	50.17			46.49	50.17	1.71	1.69			1.71	1.69
Various*	5	4	1	6.7	1.18	7.06	0.99	5.24		222.38	126.84	172.47	69.63	422		11.78	7.23	8.93	3.91	23.2	
Koko	24	20	4	5.64	1.41	5.87	1.26	4.53	1.77	127.55	101.81	126.17	102.5	134.47	113.39	5.04	4.50	4.9	4.21	5.7	6.53

The category "various" includes activities in which several producets were gathered during the same event (e.g.,* ***koko* *and fruits, mushrooms and yams, or various fruits).*

against the other gender engaging in either activity, but rather a difference in techniques and prey (Reyes-García et al., 2020). This low division of labor is a characteristic of hunter-gatherer societies (Marlowe, 2007), which the Baka appear to retain despite the adoption of a more farming-based lifestyle. That said, women do invest more than men in providing and especially preparing food, particularly the staple foods and daily meal, as also seen among the nearby Aka (Kitanishi, 2000). Although we were unable to directly measure the time and energy spent on food processing because it usually took place in camp, and was impossible to separate out from other in-camp activities in our records, we rarely observed men engaging in preparing food, except for processing nuts or when going on hunting expeditions. Moreover, women engage more frequently than men in high intensity activities such as crop harvesting, water fetching, and firewood collecting, differences that have also recently been shown among the Bayaka foragers (Sarma et al., 2020). Even if the involvement in intense activities might not relate to the overall energy spent over the day (Sarma et al., 2020), further study should explore gender differences in the energetic cost of food acquisition and preparation in relation with health among the Baka. As the Baka are currently experiencing nutritional transition (Reyes-García et al., 2019), and Baka women seem to play a key role as food providers, they might be more exposed to food insecurity, especially the older and post-reproductive women, as seen among the Aka (Robinson and Remis, 2016).

As we expected, the engagement of individuals of different ages in food acquisition activities varied. The individuals older than 60 spent less time than others in acquiring food. Instead, they spent a considerable amount of time in the settlement, resting, socializing with each other, conducting domestic chores, and especially caring for children while their parents were out of the settlement (unpublished data). Baka elders, and particularly grandmothers, play an important role in reducing the energy expenditure of their daughters, as also observed among the Aka (Meehan et al., 2013). More generally, the older cohort performs tasks that allow other age category to focus on subsistence activities, in line with what has been largely explored under the "grandmother hypothesis" (Hawkes, 2003).

Effort Required Among Food Acquisition Activities

The intensity (MET) and duration of work differed among subsistence activities. The Baka access their foods on foot, meaning that walking constitutes a large part of their daily effort and thus a large part of the time devoted to the activity, which is also seen among other societies (Christopher et al., 2019). The kilometers traveled during their activities depend on the location of the food and the total distance traveled while performing the activities itself.

The accessibility of subsistence resources varied among different activities, with firewood and water – indispensable elements for preparing food – being collected closest to the settlements. Firewood is often picked close to or in the agricultural field or the settlement, while water is fetched either in the settlement, when a water pump is present, or in the

TABLE 5 | Amount of energy dedicated to each of the gathering activities, estimated by multiplying the average energy spent in gathering a food item by the average duration of the gathering that food item (from **Table 4**), and then by the frequency of occurrence of the gathering that food item calculated by dividing the numbers in column 1 (total number of reported gathering events per food type) by the total number of observed activities (246 daily records, from **Table 3**).

		Whole sample				**Women**				**Men**			
	Total number of reported gathering events	**Number of records with MET values**	**Total Energy estimated**	**SD**	**Relative proportion**	**Number of records**	**Total energy estimated**	**SD**	**Relative proportion**	**Number of records**	**Total energy estimated**	**SD**	**Relative proportion**
Nuts	6	5	22.98	15.65	0.05	4	24.44	17.67	0.07	1	17.14	–	0.04
Yams	11	6	61.36	46.73	0.15	5	68.97	47.91	0.19	1	23.3	–	0.06
Honey	4	4	56.14	22.5	0.13	0	–	–	0.00	4	56.14	22.5	0.14
Mushrooms	9	5	25.25	22.7	0.06	3	30.49	28.21	0.08	2	17.4	16.21	0.04
Palm wine	4	2	4.47	4.1	0.01	0	–	–	0.00	2	4.47	4.1	0.01
Various*	17	5	99.5	47.31	0.24	4	86.17	42.42	0.24	1	152.85	–	0.39
Koko	50	24	149.55	135.81	0.36	20	155.34	140.9	0.43	4	120.59	119.66	0.31
Total	101	51	419.25	–	–	36	365.41	–	–	15	391.89	–	–

The category "various" includes activities in which several products were gathered during the same event (e.g.,* ***koko* *and fruits, mushrooms and yams, or various fruits).*

river close to the settlement. In contrast, accessing fishing or hunting locations required much longer distance trips. While gathering activities often required walking long distances to access particular resources, agricultural activities also required a lot of movement over long distances. While the fields might be only 1 or 2 km from the settlement, they might reach 1500 square meters in size (unpublished data). Thus, when working on their field, the Baka travel considerable distances moving back and forth within the field itself, greatly adding to the total distance required for the activity. The distance traveled in performing such activities highly depends on the environmental landscape of the settlement, which affects the time allocation pattern. For example, in other Baka settlements from Cameroon located along the Dja river, the Baka are much more involved in fishing (Oishi, 2006) than what we observed. Even in the same area, the local environment of each settlement shapes the time allocation pattern. In this study, we saw that agricultural tasks involved the lowest durations in Le Bosquet, in part due to the limited distance people from this settlement had to travel to their fields (an average of 6.4 km). Agricultural tasks took more time in other villages, where people either had their field further from their settlement, or worked more often in distant Nzime fields (Elonda 10.3 km, Kungu 8.4 km, and Mombokola 7.22 km).

Given the relatively long distances traveled for subsistence activities, it is not surprising that the Baka combine different tasks in one trip. Either planned or opportunistic, these combined activities might be an effective way to optimize their energy use. Moreover, many subsistence activities also provide benefits not directly related to nutrition, such as social sharing (sharing of stories or daily worries), transmission of traditional knowledge, and development of sexual identity and gender roles (Gallois and Duda, 2016), which are key aspects for the social cohesion of the communities (Joiris, 1992) and the cultural evolution among humans (Gurven and Kaplan, 2006).

The actual intensity of work needed for acquiring food varies, as shown by the variability of the MET according to the activity performed (**Table 2**). Some emic and ethnographic insights might explain why some activities are more effort demanding than others. When we asked the Baka which activity was the most difficult, they reported cutting trees. This occurs on several different occasions: when opening new fields, gathering firewood, and collecting honey. The Baka customarily burn and cut some of the large living trees when opening a new field. As it occurs mostly during both dry seasons, periods in which we collected some of the data, this may contribute to the high MET value recorded for agricultural work. Also, they occasionally cut standing dead wood as it is considered to be better fuel than fallen wood. This might contribute to the large costs seen in firewood gathering. Lastly, they often cut down trees in which bees are nesting instead of climbing the tree. While this activity would have increased the average energy spent on gathering activities, all of the honey collected during our study period was from bees that nest in already-fallen trunks, so no trees were cut down. We also suppose that the high MET values of crop harvesting, water fetching and firewood collection relate to the heavy loads the Baka transport, in baskets carried on their heads that can reach about 20–30 kg (unpublished data). Further studies should explore in detail the relative effort demanded for the different tasks conducted in these activities. Using both heart rate monitors and focal follows might be a useful method for better understanding the drivers of the effort demanded within the different food acquisition activities.

Crucially, we found that hunting has a lower MET than does gathering. While hunting requires complex skills and knowledge (Gurven and Kaplan, 2006; Duda et al., 2017), the techniques used by the Baka in our records do not require as high intensity of work, as measured by MET, as other activities, especially gathering. When comparing hunting techniques, we do note that pursing game with either spears or guns had a lower MET than when using snares (**Table 2**). However, because we have relatively few records of hunting, these results may not be representative. Some hunting expeditions, especially those taking place at night, might be longer than those we measured. An average of 8 h has been recently reported in other Baka settings (Martin et al., 2020). Longer hunting trips would increase the overall energy spent, but the average intensity of work might not be much higher, as most of the time is spent walking. The hunting of large mammals, which might imply periods of high level of effort, is nowadays almost never performed by the Baka (Duda et al., 2017). Therefore, the low average MET we report might nevertheless be representative of the Baka's present-day hunting techniques.

Finally, most of the energy seems to be devoted to agriculture and gathering. This mixed strategy may help provide better nutrition (Milton, 2000; Yamauchi et al., 2000) and allow forager societies to be less at risk of famine than their neighboring farmers (Berbesque et al., 2014). However, the engagement in this mix of farming and foraging activities varies according to the settlements, which have diverse socio-economic and ecological contexts. This includes the accessibility of the resources, as discussed earlier, and also the proximity to Bantu villages, their market integration, the exposure to outsiders, etc. While the performance of agriculture seems to be a general pattern, the subsistence strategy is a local decision made within a particular socio-ecological context. Livelihood strategies among former foragers in a changing context depend on several interrelated ecological, social, and economic factors, and also on individual and familial decisions. In the same village, some households might focus more heavily on foraging, others on farming, others on wage labor, while some seem to mix all kinds of activities (Reyes-García et al., 2017). Thus, as these groups might demonstrate "*astute awareness of changing opportunities and often develop ways to take advantages of novel resources, technologies and interactions with non-foraging neighbors*" (Codding and Kramer, 2016, p. 40), it is necessary to take a multivariable approach when looking at changes in local livelihood and culture in this global context. This kind of approach may help explain the variable and non-linear patterns of the adoption of agriculture observed in other places and times in human history (Codding and Kramer, 2016).

Specificities and Characteristics of Gathering Activities

Gathering was one of the most frequent activities within Baka daily life, and was performed by both men and women. Men regularly engage in gathering not only high risk foods such as honey (Marlowe et al., 2014) or high energy foods like nuts (Sillitoe, 2002), but also in foraging for leaves, mushrooms, and other foods such as palm wine and caterpillars. In line with studies among different hunter-gatherer societies showing that men considerably invest in gathering (Panter-Brick, 2002; Bird et al., 2012), and that men target the same or similar foods as women do (Lee and DeVore, 1973), our results further confirm the involvement of both genders in gathering.

Overall, gathering implies considerable intensity of work, as the average MET for gathering activities was higher than those of both hunting and fishing. Moreover, it is not a homogeneous task, with a higher variability in MET values than any other activity, and with significant differences in MET among food items (**Table 4**). Gathering subsumes a large number of different techniques, amounts of time spent, and effort expended. This variability might be explained regarding the diverse products and their related gathering techniques.

Some wild foods, such as **koko** leaves, mushrooms, and fallen fruits and seeds require the gatherer to only collect the edible parts, while other products need more tools and processes. Notably, gathering activities of two most energetically dense foods consumed by the Baka, fat-rich nuts and starch yams, have the highest MET values among all subsistence activities measured. For the fat-rich seeds, the gatherer also has to extract the kernel, which involves significant time and intensity of work. This is the case for 10 different species, including *P. oleosa*, *Irvingia* spp., *Klainedoxa* spp., *Baillonella toxisperma, Poga oleosa*, and *Pentaclethra macrophylla.* The gathering of yams (about ten different species of *Dioscorea*) requires deep digging to access the edible tubers, often with specialized tools and knowledge (Dounias, 2001). Therefore, the effort of the gathering activities directly depends on the resources targeted within the large range of available foods.

To more fully understand the relationship of gathering effort among different food types, future research should focus on the caloric and nutrient returns from gathering expeditions. While the nutritional values of some plants have been described (see for instance Hladik, 1996), most of the plants from the Baka region are understudied. This lack of detailed nutritional information is unfortunately still a problem for most wild plants eaten by hunter-gatherer groups (Pontzer and Wood, 2021). Furthermore, the studies that have been carried out indicate that there is a high degree of nutritional variability even within a single taxon, such as within **koko** (Ali et al., 2011). Such variability suggests that highly detailed nutritional studies need to be coupled with foraging return rates in order to accurately explore the place of wild food in Baka diet and more generally on forager-horticulturalist foraging behavior and diet.

Beyond their nutritional benefits, plant foods and gathering also have value in a cultural and social context. Studying socio-cultural elements might provide insights on the reasons that the Baka gather different wild plants. The collection and consumption of some plants might relate to local perceptions toward food (De Garine, 1996), which then drive subsistence strategies. For example, the frequently consumed **koko** leaves were listed as both a preferred food and a "prestigious" food (i.e., a food that the Baka would prepare when receiving an important guest), while no other wild leaf was mentioned as such (Gallois et al., 2020). The yams also play an important role in the Baka cosmology (Dounias, 2001), which may contribute to their continued use of these foods despite access to potentially more-energy-dense domesticated tubers. For the Baka, the fatty nuts foster a feeling of abundance and satiety, which is intimately related to their concept of "well-eating" (Joiris, 1996). However, the gathering of these nuts is also driven by economic considerations such as opportunities to earn money because they are often targeted by traders (Gallois et al., 2020). Therefore, a higher integration to the market does not necessarily imply a decrease of gathering activities, as also reported elsewhere (Codding and Kramer, 2016). Due to the different potential factors driving both the collection and the consumption of wild plants, it seems crucial to settle any study, whether focused on energetics, nutrition, socio-cultural effects, or ecology, in the overall complex context in which the society has developed. Considering the general pressures influencing local societies and environments, the cost of gathering is not only spent for providing food to the local communities but also as a part of the global market, with the potential consequences of overexploitation of natural resources.

CONCLUSION

While gathering is often characterized as an easy activity, we found that it requires considerable effort in comparison with other subsistence activities, and that the costs vary depending on the food targeted. Studies that work with contemporary societies in order to understand universal patterns of human behavior should consider exploring the variability of techniques and related effort within each subsistence activity. Finally, socio-cultural contexts and individual decisions are crucial elements for understanding how foraging societies are adapting their livelihood and culture in this era of rapid global changes.

AUTHOR'S NOTE

Sandrine Gallois (Ph.D. in Environmental Science and Eco-Anthropology, 2016) is a post-doctoral research fellow at Leiden University, the Netherlands. Her research focuses mostly on human environment relations including the acquisition of local ecological knowledge in a context of global change. Taking an interdisciplinary approach, her areas of interest are biocultural diversity, cultural transmission, childhood, ethnobotany, social-ecological systems, and science-policy interface.

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DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by this study adheres to the Code of Ethics of the International Society of Ethnobiology, and received the approval of both the Ethics Committee of Leipzig University (196-16/ek) and the Ethical Committee from the Ministry of Health of Cameroon (n°2018/06/1049/CE/CNERSH/SP). Before the onset of the study, we obtained Free Prior and Informed Consent (FPIC) from every individual taking part of this research. Explanation of the project and individual consent was audio recorded, since many of the participants were illiterate. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

Both authors designed this study and wrote the final manuscript. SG collected, processed, and analyzed the data from all field seasons. AH collected data in the first field season, performed the GLM analyses, and contributed to other analyses of the data.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.768003/full#supplementary-material

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Cost-Benefit Trade-Offs of Aquatic Resource Exploitation in the Context of Hominin Evolution

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While the exploitation of aquatic fauna and flora has been documented in several primate species to date, the evolutionary contexts and mechanisms behind the emergence of this behavior in both human and non-human primates remain largely overlooked. Yet, this issue is particularly important for our understanding of human evolution, as hominins represent not only the primate group with the highest degree of adaptedness to aquatic environments, but also the only group in which true coastal and maritime adaptations have evolved. As such, in the present study we review the available literature on primate foraging strategies related to the exploitation of aquatic resources and their putative associated cognitive operations. We propose that aquatic resource consumption in extant primates can be interpreted as a highly site-specific behavioral expression of a generic adaptive foraging decision-making process, emerging in sites at which the local cost-benefit trade-offs contextually favor aquatic over terrestrial foods. Within this framework, we discuss the potential impacts that the unique intensification of this behavior in hominins may have had on the evolution of the human brain and spatial ecology.

Keywords: foraging strategies, non-human primates, decision-making, spatial ecology, cognition, brain size

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INTRODUCTION

Under the framework of optimal foraging theory (Stephens and Krebs, 1986), animals are thought to have evolved foraging strategies that increase individual fitness by maximizing the benefits while minimizing the costs and risks related to the exploitation of resources in their natural habitats (Charnov, 1976). In turn, the outcomes of this optimization are suggested to be reflected in a variety of observable behaviors and domains, such as spatial ecology (Pyke, 2019b; Tórrez-Herrera et al., 2020), patch use (Bedoya-Perez et al., 2013) and dietary preferences (Harris et al., 2019). Accordingly, the evolution of foraging strategies must be accompanied by the evolution of (i) cognitive abilities that allow for a contextual computation of costs and benefits resulting in the decision-making processes expressed as behavior (Rosati, 2017) and (ii) their specific neuroanatomical correlates, such as overall brain size (e.g., DeCasien et al., 2017) or the size of specific brain regions involved in those processes (e.g., Louail et al., 2019). As such, considering this framework for investigating the underpinnings of differences in foraging niches and territorial occupation patterns between primate species, and its application in the context of human evolution may provide essential insights on what mechanisms have allowed hominins to inhabit an unmatched variety of ecosystems when compared to non-human primate species.

In this context, two main hypotheses have been formulated to link the decision-making challenges primates face in the wild to the evolution of their complex cognition and brain size: the social and ecological brain hypotheses. According to the former (Dunbar, 1998; Dunbar and Shultz, 2007), cognitive challenges associated with living in large, complex social groups require individuals to keep track of and act on a broader record of competitive and cooperative interactions, which in turn generates selective pressures for adaptive cognitive traits (Byrne, 1996; Brosnan et al., 2010; Massen et al., 2014). As such, the increase in social complexity would comprise the most expressive selective force acting on the evolution of primate cognition and, in turn, of their brain size (Jolly, 1966; Humphrey, 1976; Dunbar, 1998). The second hypothesis, i.e., the ecological brain hypothesis, seeks to explain the evolution of brain size and complex cognition primarily using ecological proxies (Milton, 1981, 1988; Rosati, 2017). In this context, the evolution of cognitive traits related to decision-making, spatial memory and executive control, for example, would be adaptive toward optimizing the trade-offs between costs and benefits of foraging in complex and fluctuating environments (Rosati, 2017; Garcia et al., 2021). In support of this hypothesis, a recent study by DeCasien et al. (2017) using data from a wide diversity of primate species provided evidence that diet is a better predictor of total relative brain size in primates—an measure for global cognitive skills (Deaner et al., 2007; Shultz and Dunbar, 2010)—when compared to social variables, such as group size. Nonetheless, recent research has demonstrated that overall brain size can be a poor proxy for studying the development of specific cognitive skills related to foraging ecology and sociality (Louail et al., 2019). Moreover, it is important to note that these two hypotheses are not mutually exclusive, and each of them can be better at explaining different aspects of primate cognition (Cunningham and Janson, 2007; Rosati, 2017). In this sense, social proxies may be better suited to explain the evolution of cognitive skills related to social learning, for example, and ecological factors, in contrast, may offer a higher explanatory power for the evolution of cognitive skills related to foraging and dietary preferences (Ban et al., 2016; Janmaat et al., 2016; Trapanese et al., 2019). This observation is consistent with evidence presented by DeCasien and Higham (2019), suggesting that the mosaic brain evolution observed in primates is linked to niche specialization, with the evolution of the size of different brain regions being selected according to specific ecological characteristics of distinct primate species (Louail et al., 2019).

Several recent studies aimed at assessing the evolution of cognitive skills involved in finding and exploiting high-quality ephemeral resources in complex terrestrial environments (e.g., Janmaat et al., 2014; Ban et al., 2016; Salmi et al., 2020). In densely forested tropical ecosystems, for example, high-energy foods, such as fruits, may be sparsely distributed and difficult to find, making food search a highly costly activity (Janmaat et al., 2016). As such, the goal of optimal foragers inhabiting these areas is to increase their intake yield while minimizing the energetic expenses derived from food search (Schoener, 1971). One way chimpanzees (*Pan troglodytes*) have been demonstrated to achieve this is via the modulation of their navigation strategies through the use of less energetically demanding paths when moving between sparsely distributed food sources (Green et al., 2020). In addition, chimpanzees are also known to plan their nest departure time according to the availability, nutritional quality and location of seasonal food resources (Janmaat et al., 2014). However, in the context of energetic optimization, some high-risk, high-yield items such as high-trophic level aquatic resources (both marine and riverine/lacustrine) could also hold major importance in the regulation of energetic balance of primates (Cunnane and Stewart, 2010; Koops et al., 2019), but have been rather overlooked compared to terrestrial resources. This focus on terrestrial resources, albeit partly rooted in the fact that most non-human primate species inhabiting coastal or flooded areas do not forage on aquatic resources (Nowak et al., 2019), may have caused researchers to overlook the relative importance of this behavior in the evolution of some primate species, and particularly in hominins. As pointed out by Archer et al. (2014), for example, the components of archeological assemblages related to aquatic fauna have been far less studied as evidence of early hominin exploitation when compared to terrestrial components, even when the two are found at the same site. As such, this type of issue creates a bias in our reconstruction of the niches occupied by extinct hominins and extant primates, leading to gaps in our understanding of how the consumption of aquatic resources may be linked to the evolution of brain size and cognition in these groups.

Thus, the purpose of this literature review is to discuss primate foraging strategies and their putative associated cognitive operations related to the exploitation of aquatic resources, as well as their implications in the evolution of the primate brain. As such, firstly we present some of the main patterns observed in the aquatic foraging behavior of non-human primates. Then, we review the costs and benefits related to the consumption of aquatic resources, with a particular focus on how marine and freshwater resources contrast with terrestrial resources in their contribution to the energetic optimization in extant non-human primates. We also consider the evidence for intentionality in the exploitation of aquatic resources by hominins and non-human primates and, as such, the extent to which their associated behaviors take place in a planned or opportunistic fashion. In addition, we also aim to specify the potential cognitive operations involved in foraging for aquatic resources, and evaluate the correlation between the evolution of such skills and neuroanatomical changes during the course of human evolution. Finally, by examining the evidence for the emergence of true coastal adaptation in hominins, we aim to assess the implications of the exploitation of coastal resources in the context of territorial occupation, movement ecology, technological complexity and social behavior, as well as the relation of such novelties with the evolution of complex cognitive skills. Overall, the present review seeks to set the foundation for future research attempting to ratify evolutionary interrelationships between aquatic resource exploitation, cognitive ecology and neuroanatomy in extant primates and extinct hominins.

PATTERNS IN THE EXPLOITATION OF AQUATIC RESOURCES BY NON-HUMAN PRIMATES

While several primate species that inhabit flooded areas exhibit aquatic behaviors that are relevant to aspects of their ecology, only a fraction of them seems to forage on aquatic foods (Nowak et al., 2019). Together, the five main reviews on the use of aquatic resources by non-human primates show that a total of 26 species (i.e., about 4% of the existing non-human primate species) feed on aquatic fauna (Stewart et al., 2008; Kempf, 2009; Stewart, 2010; Russon et al., 2014; Nowak et al., 2019), out of which ten are found to feed on fish (Russon et al., 2014; Mallick, 2019). Since their publication, developments in this field have caused this number to increase, for example with the first evidence of regular consumption of aquatic fauna (i.e., crabs) by a population of chimpanzees in the Nimba mountains, Guinea (Koops et al., 2019). Still, the total number of species that exploit aquatic resources in general—including fauna and flora—remains disputed, as no systematic reviews are available on the consumption of aquatic flora by primates (Russon et al., 2014). Nevertheless, aquatic foraging has been well documented in several species—e.g., chimpanzees (Nishida, 1980; Sakamaki, 1998; Devos et al., 2002), bonobos (Hohmann et al., 2019), chacma baboons (Lewis et al., 2018) and long-tailed macaques (Tan et al., 2015; Tan, 2017)—leading to speculation on its relative importance for the ecology of a variety of primate groups, and ultimately in the context of hominin evolution (e.g., Boesch et al., 2017; Hohmann et al., 2019; Koops et al., 2019).

Although the exploitation of aquatic fauna and flora may involve distinct acquisition and extraction processes, a few general patterns emerge from the available records of aquatic resource consumption by extant non-human primates. Firstly, behaviors associated with aquatic resource exploitation tend to be highly site-specific, independently of the type of food consumed (**Table 1**). In chimpanzees, for example, the consumption of aquatic fauna has only been observed in the Nimba mountains (Koops et al., 2019), in spite of the existence of several long-term field projects dedicated to the study of this species *in situ* (e.g., Pusey et al., 2007; Boesch et al., 2019; Thompson et al., 2020)—also including nearby locations, such as Bossou (Humle et al., 2011; Koops et al., 2019; Matsuzawa, 2019). Notably, the chimpanzee populations in these two locations also differ in their consumption of aquatic flora: while individuals at Bossou have been observed engaging in algae scooping—a behavior characterized by using sticks to scoop algae from water bodies (Matsuzawa, 1996; Humle et al., 2011)—the chimpanzees at Nimba have not (Matsuzawa, 2019). As such, the disparity in observed aquatic foraging behaviors in these two locations has been hypothesized to be a product of differences in resource availability within the ranges of both chimpanzee groups, given the absence of shallow freshwater streams with crabs at Bossou and the scarcity of ponds with algae at Nimba (Matsuzawa, 2019). Nevertheless, chimpanzees represent only one example of the site-specificity of the consumption of aquatic fauna and flora in primates. Differences in aquatic fauna exploitation have been described between chacma baboons troops (*Papio ursinus*) living at Cape Reserve—which fed on marine invertebrates (Hall, 1962; Lewis and O'Riain, 2019)—and groups inhabiting the Namib desert, which fed on fish from drying desert pools (Hamilton and Tilson, 1985). In addition, this pattern can also hold true for certain species of Pan-American monkeys, such as bearded capuchins (*Sapajus libidinosus*), which have also been recorded to forage on either marine invertebrates (Santos et al., 2019b) or fishes (Mendes et al., 2000), depending on the studied site.

Secondly, the exploitation of aquatic resources in a variety of sites can also be dependent on demographic and individual factors. This is the case for Orangutans living in a fresh-water island habitat in Borneo, Indonesia, for example, where aquatic foraging behavior depends on individual age and water skills (Russon et al., 2014). At this site, all the individuals who were observed to engage in fish catching and eating were juveniles or adolescents. In this context, Russon et al. (2014) suggested that this pattern may be related to the innovative character of juvenile and adolescent primates, which has been well documented in previous research (e.g., Reader and Laland, 2001; Russon et al., 2010). In addition, orangutan individuals who consumed fish were also more skilled in the water compared to others at the same site (Russon et al., 2014), providing evidence that previously acquired skills of individuals can also affect the development of behaviors involved in aquatic resource exploitation. Furthermore, demographic factors have also been demonstrated to affect the consumption of aquatic crabs by chimpanzees at the Nimba mountains (Koops et al., 2019), where females and infants were found to forage for crabs more frequently and for longer periods when compared to adult males, which was hypothesized to be linked to their reduced access to game meat (Koops et al., 2019).

Thirdly, the exploitation of aquatic resources in primates may or may not rely on the use of tools (**Table 1**), depending on the species and individual skills. Several species of extant non-human primates have been recorded to exploit aquatic foods using external tools (Russon et al., 2014). A notable example outside of the great apes are Burmese long-tailed macaques (*Macaca fascicularis*), which employ a variety of stone-hammering techniques for obtaining aquatic foods in coastal environments (Tan et al., 2015; Gumert et al., 2019). For each of these techniques, individuals may employ distinct manual skills, in addition to selecting tool types according to their suitability for the intended task (Gumert et al., 2009; Tan et al., 2015). Besides its specificity regarding the target food item, tool-assisted aquatic resource foraging techniques can also vary within species across different locations. For example, bearded capuchins have been documented to employ different tool-assisted foraging techniques to obtain aquatic foods in distinct study sites, such as the use of baits to prey on fish (Mendes et al., 2000) and shell cracking through percussion (Santos et al., 2019b). In the first case, fishing capuchins would either place food baits under water or hold them partially submerged to

TABLE 1 | Cited examples of aquatic resource consumption by non-human primates.

Study site	Consumed resource type	Habitat type	External tool use observed?	Sources
Chimpanzee *(Pan troglodytes)*				
Bakoun, Guinea	Aquatic algae	Mosaic forest	Yes	Boesch et al., 2017
Bossou, Guinea	Aquatic algae	Mosaic forest	Yes	Matsuzawa, 1996; Humle et al., 2011; Matsuzawa, 2019
Nimba mountains, Guinea	Freshwater crabs	Medium-altitude evergreen forest	No	Koops et al., 2019
Lokoué Bai, Republic of Congo	Aquatic algae	Forest clearing	Yes	Devos et al., 2002
Mahale mountains, Tanzania	Aquatic algae	Low-altitude forest	No	Nishida, 1980; Sakamaki, 1998
Bonobo *(Pan paniscus)*				
LuiKotale, Democratic Republic of the Congo	Aquatic algae	Mosaic forest	No	Hohmann et al., 2019
Bornean orangutan (*Pongo pygmaeus*)				
Kalimantan, Indonesia	Fish	Forested island	Yes	Russon et al., 2014
Chacma baboon (*Papio ursinus*)				
Cape peninsula, South Africa	Mussels, limpets, crabs, sealice, shark eggs	Coast	No	Hall, 1962; Lewis et al., 2018; Lewis and O'Riain, 2019
Namib desert, Namibia	Fish	Desert waterholes	No	Hamilton and Tilson, 1985
Long-tailed macaque (*Macaca fascicularis*)				
Laem Son National Park, Thailand	Marine mollusks, crustaceans, fish, chiton, aquatic plants	Rocky shores, sandy beaches, mangrove	Yes	Malaivijitnond et al., 2007; Gumert et al., 2009; Gumert and Malaivijitnond, 2012; Tan et al., 2015; Gumert et al., 2019
Sam Roi Yot National Park, Thailand	Marine invertebrates	Rocky shores, sandy beaches	Yes	Tan, 2017
Rhesus macaque (*Macaca mulatta*)				
Sundarbans, India and Bangladesh	Mollusks, crabs and fish	Mangrove	No	Mallick, 2019
Japanese macaque (*Macaca fuscata*)				
Kinkazan island, Japan	Seaweeds and mollusks	Coast	No	Tsuji and Kazahari, 2019
Green monkey (*Chlorocebus sabaeus*)				
Saloum delta, Senegal	Crustaceans and mollusks	Mangrove	No	Galat and Galat-Luong, 1976; Head et al., 2019
Bearded capuchin (*Sapajus libidinosus*)				
Parque Zoológico de Goiânia, Brazil	Fish	Captive environment	Yes	Mendes et al., 2000
Rio Preguiças, Brazil	Snails, crabs and shipworms	Forest fragments	Yes	Santos et al., 2019b

attract pond fish, subsequently assuming a fishing body posture that allowed the individual to observe and attempt to capture approaching fishes that were attracted to the bait (Mendes et al., 2000). Invertebrate foraging individuals, on the other hand, used branches as hammers to crack the shells of marine invertebrates in order to forage on them (Santos et al., 2019b). Nevertheless, similarities in techniques used for foraging on aquatic resources have also been observed across sites located at great distances from each other, showing that some of these behaviors can also be geographically widespread. This is the case in some chimpanzee populations which have been observed to employ comparable scooping on foraging for algae in a variety of sites throughout Western (Matsuzawa, 1996; Boesch et al., 2017) and Central Africa (Devos et al., 2002), all of which included some form of tool selection or modification.

Lastly, alike other innovations, behaviors related to the exploitation of aquatic foods can be invented, lost, independently reinvented, acquired through social learning and adapted to and from other tasks unrelated to aquatic foraging (Nishida et al., 2009; Shumaker et al., 2011; Russon et al., 2014; Bandini and Tennie, 2017; Luncz et al., 2017; Mallick, 2019; Santos et al., 2019b). Therefore, in some cases, such behaviors can potentially develop into local traditions with respect to (i) the social position of individuals partaking in it (e.g., Koops et al., 2019), (ii) the type of resource consumed (Matsuzawa, 1996, 2019; Koops et al., 2019), and possibly (iii) the technique used to obtain it (e.g., algae feeding behavior as described in Sakamaki, 1998; Devos et al., 2002; Boesch et al., 2017, albeit the evidence described in Sakamaki, 1998 stems from only one female chimpanzee who was hypothesized to have acquired her distinct algae feeding behavior from her natal group). Furthermore, aspects of exploiting aquatic foods in non-human primates may not only be socially learned from conspecifics, such as shellfish cracking techniques in long-tailed macaques (Tan, 2017), but also be facilitated or primed by the behavior of individuals from other species, such as *Homo sapiens* (reviewed in Russon et al., 2014). Finally, in some cases, such as in long-tailed macaques, the exploitation of aquatic resources can encompass a variety of local traditions (Tan et al., 2015). Thus, alike other behaviors associated with foraging for terrestrial resources (e.g., tool use; Whiten et al., 1999; Whiten and van de Waal, 2017), it might be hypothesized that, in some cases, the exploitation of aquatic resources by extant non-human primates can be interpreted as a cultural phenomenon, adding to the portfolio of socially transmissible behavioral strategies that different species and populations have developed to forage more optimally on locally available resources.

TRADE-OFFS BETWEEN AQUATIC AND TERRESTRIAL FORAGING

The nature and the importance of aquatic resource exploitation in the context of primate feeding ecology remains a contested topic, as many species of primates that live nearby water bodies or flooded areas often do not feed on aquatic foods (Nowak et al., 2019). Thus, the precise mechanisms through which the consumption of aquatic resources can be beneficial for and influence selection in primate populations remains largely unknown (Hohmann et al., 2019). In addition, the site-specificity of the types of resources consumed, of the demographics of who consume them and of the employed techniques hinders general interpretations of the value of such behavior. Nevertheless, within the framework of optimal foraging theory, there may be several potential ways in which foraging for aquatic resources can be a useful behavioral strategy toward energetic optimization in non-human primates.

Firstly, the nutritional benefits of aquatic fauna consumption would include increased intake of long-chain polyunsaturated fatty acids (LC-PUFAs), which have been regarded as important for the development and function of large primate brains (Joordens et al., 2014). In this sense, the intake of eicosapentaenoic acid (EPA) and arachidonic acid (AA) would be specially increased with aquatic fauna consumption, as these nutrients are rare in terrestrial foods, with the exception of the fatty parts of meat and the brain tissue of some animals (Li et al., 1998; Cordain et al., 2002; Carlson and Kingston, 2007; Stewart, 2010; Joordens et al., 2014). However, brain tissue can be costly to extract, and given the evidence for the health risks associated with its consumption in humans, such as prion diseases (Berger et al., 1997; Domachowske and Suryadevara, 2020), and the susceptibility of non-human primates to such diseases (Dalsgaard, 2002; Race et al., 2009), acquiring EPA and AA through the consumption of brain tissue may not represent an optimal strategy when compared to aquatic fauna. In addition, obtaining fresh terrestrial animal tissue through hunting can be highly energetically costly, dangerous (Boesch, 1994; Tennie et al., 2014) and carry the associated risk of failure (Boesch and Boesch-Achermann, 2000; Gilby and Wrangham, 2007). Comparatively, foraging on some aquatic resources such as mollusks and arthropods can represent a less risky and more energetically efficient alternative to obtain LC-PUFAs for some non-human primates, especially considering the relative abundance and ease of access to these resources in some sites (e.g., Malaivijitnond et al., 2007; Koops et al., 2019). In this sense, this behavior could be particularly advantageous for non-human primate populations that exhibit relatively low hunting opportunities (Koops et al., 2019), and for individuals who have less access to hunting meat, such as females and infants (Fahy et al., 2013; Gilby et al., 2017). Nevertheless, other brain-essential LC-PUFAs, such as docosahexaenoic acid (DHA), can also be metabolically synthesized from precursors, but the relative importance of their dietary uptake vs. their synthesis in the context of brain development remains unclear, and should be experimentally addressed in future studies (Joordens et al., 2014; Koops et al., 2019). Moreover, the quantities of EPA, DHA, and AA found in aquatic fauna can be tied to local conditions, and as such it may vary over time, space and according to the species consumed (Joordens et al., 2014).

Furthermore, it has been hypothesized that the consumption of aquatic flora is important for ensuring sufficient uptake of certain minerals like iodine (Hohmann et al., 2019). Iodine is essential for numerous physiological and developmental functions, including brain development, due to its influence on thyroid function (Venturi and Bégin, 2010). It can be abundant in a diversity of ecosystems, such as coastal and volcanic areas, as well as wetlands (Hohmann et al., 2019). In other terrestrial habitats such as rainforests, on the other hand, access to iodine can be limited (World Health Organization, 2007), with health issues tied to iodine deficiency occurring at relatively high rates in some human populations inhabiting these areas (Phillips et al., 1988; Vanderpas and Moreno-Reyes, 2017). Given the similar detrimental effects that iodine deficiency can have in humans and non-human primates (Mano et al., 1987), it is reasonable to assume that developing a way to access iodine in these iodine-poor environments would be advantageous, and possibly confer a fitness advantage. In this sense, Hohmann et al. (2019) have demonstrated that aquatic algae can provide a rich source of iodine for primates living in rainforest environments, and that a population of bonobos (*Pan paniscus*) at the Congo basin regularly consumed aquatic herbs as part of their diet. In addition, aquatic algae were found to contain higher levels of several essential minerals (i.e., Mn, Ca, Mg, Fe, K, and I) when compared to ripe fruits and terrestrial herbs (Hohmann et al., 2019). Other species of apes also feed on aquatic herbs (Kempf, 2009), and the potential importance of aquatic plants as sources of minerals in primate diets has also been proposed by other authors (e.g., Boesch et al., 2017).

In this context, given the diverse nature of behaviors linked to aquatic resource exploitation in non-human primates, the costs and benefits of consuming these items have also been hypothesized to vary temporally, spatially and across sex and age. Long-tailed macaques, for example, show higher rates of aquatic foraging during periods when the abundance of ripe fruit is reduced (Yeager, 1996; Malaivijitnond et al., 2007). In this case, the consumption of aquatic resources could potentially serve as a fallback source of nutrients in periods when other food sources are scarcer (Stewart, 2010). In Bakoun, Guinea, fishing for algae among chimpanzees is frequent during the dry season and absent during the wet season (Boesch et al., 2017). Aquatic algae is a highly preferred food item at this site, which has been suggested to play an important role in satisfying chimpanzee dietary requirements by providing a source of protein, carbohydrates, lipids and minerals (Becker, 2007; Tipnee et al., 2015; Boesch et al., 2017). Given the limited availability of aquatic algae in Bakoun, which is restricted to the dry season, its frequent consumption during such periods likely represents a more optimal behavioral strategy considering the otherwise limited access to abundant terrestrial foods and water at this location (Boesch et al., 2017). Contrastingly, in sites where ponds with aquatic algae are scarcely found, algae foraging behavior would likely incur higher search costs and lower yields, which in turn would not be as energetically profitable. This is the case for chimpanzees inhabiting the Nimba mountains, where algae scooping behavior has not yet been observed (Matsuzawa, 2019), and instead chimpanzees feed on aquatic crabs, which are more widely available and likely represent a more optimal local foraging strategy (Koops et al., 2019; Matsuzawa, 2019). Unlike the aquatic algae foraging in Bakoun, crab consumption on Nimba mountains chimpanzees occurs independently of seasonality, and is instead dependent on demographic factors, with females and infants engaging in this behavior significantly more often than adult males (Koops et al., 2019). In this context, Koops et al. (2019) proposed that the associated benefits of crab foraging for females may be linked to an increase in access to salts. In addition, given the small size of the majority of crabs found at this site (Koops et al., 2019), crab fishing also poses less injury risks when compared to hunting (e.g., getting wounded; Busse, 1977) and ant-dipping (e.g., suffering painful bites; Humle et al., 2009). As such, this activity could be suitable for immature individuals practicing their foraging skills (Koops et al., 2019).

Nevertheless, foraging on aquatic resources is not devoid of associated risks. Freshwater crabs, for example, may be a source of parasites that cause human lung fluke disease, which is known to also affect non-human primates (Sachs and Voelker, 1975; Voelker and Sachs, 1977; Friant et al., 2015). Moreover, primates in close proximity to water bodies may be susceptible to predators such as crocodilians in some environments (Cowlishaw, 1994; Hill and Dunbar, 1998; Cheney et al., 2004). At coastal sites, primates engaging on aquatic foraging may also face challenges related to accessing frequently submerged food items (e.g., mollusks and invertebrates). The predation of marine organisms by chacma baboons in the intertidal zone at the Cape Peninsula, for example, has been negatively correlated to increases in risks associated to coastal foraging (e.g., wave height, offshore wind speed and increasing tides; Lewis and O'Riain, 2019). In addition, the use of flooded habitats may also involve increases in energetic costs associated with thermoregulation (Head et al., 2019) and with the extension of ranging areas and travel distances (Santos et al., 2019a). In this context, such cost-benefit trade-offs may be more likely to affect aquatic foraging when the relative payoff of such behavior is higher. In line with this premise, a recent study on Japanese macaques (*Macaca fuscata*) has found that their seafood feeding behavior is only linked to tidal cycles in months when forests are poorer in resources, favoring behaviors that increase the efficiency of aquatic resource exploitation (Tsuji and Kazahari, 2019). Finally, in some cases, the exploitation of aquatic foods can also involve high extraction costs, especially when it concerns the consumption of encapsulated foods (e.g., shelled mollusks and crustaceans). To counter this issue, some non-human primate populations resort to the use of percussive tools, presumably to increase the efficiency of the acquisition of aquatic resources (Gumert et al., 2019; Santos et al., 2019b). Such use of percussive tools in the context of aquatic foraging can be cognitively demanding (Santos et al., 2019b), which may help to explain why this behavior has only been observed in species for which the use of percussive techniques for the extraction of encapsulated forest foods has also been recorded: long-tailed macaques (Gumert et al., 2019) and bearded capuchins (Santos et al., 2019b). Nevertheless, it is important to note that there are also examples of other non-human primate species that are able to intensively exploit shelled aquatic resources without using external tools, such as green monkeys (Galat and Galat-Luong, 1976; Head et al., 2019) and rhesus macaques (Mallick, 2019).

INTENTIONALITY IN THE CONSUMPTION OF AQUATIC RESOURCES

Within the framework of the optimal foraging theory, individuals would evolve cognitive skills that allow them to exhibit more efficient foraging decision-making strategies in their local environment (Charnov, 1976; Stephens and Krebs, 1986; Pyke, 2019a). Thus, when the benefits of exploiting aquatic resources outweigh its risks and costs, it can be expected that this behavior will take place intentionally (i.e., as the expected outcome of a decision-making process) rather than opportunistically (i.e., via a set of simple reflexes based on direct perceptions that enable animals to maximize intake and minimize costs without any cognitive operation). In this sense, while some non-human primate species have been shown to make use of aquatic habitats intentionally, for example, for predation avoidance choice (see Otani et al., 2020), establishing the intentionality of aquatic resource exploitation would require evidence for planning and anticipation of a specific feeding event by an individual. In this context, although it has been suggested that deliberate aquatic resource consumption in primates can be detected from search behavior (Russon et al., 2014), the most reliable available proxy to establish intentionality is likely tool selection followed by tool use.

In order to select, prepare and flexibly use tools, animals need both to understand causality and to be able to plan sequences of actions (Musgrave and Sanz, 2019). In other words, when an individual selects and uses a tool for foraging, it must first be able to anticipate the required task to obtain the intended resource, subsequently engaging with the chosen tool in a way that is suitable for accomplishing the envisioned goal. Algae-scooping chimpanzees in Bossou, for example, are known to preferably use fern stalks when manufacturing the sticks that are used to retrieve algae from ponds, which in turn has been hypothesized to be due to its suitability for the task, as the small hooks on fern stalks may increase algae gathering efficiency (Matsuzawa, 2019). Likewise, long-tailed macaques are known to select aquatic foraging tools according to their intended use, employing different techniques depending on prey species (Gumert et al., 2009). Additionally, tool-use has been suggested to depend on the prior computation of the relative costs and benefits of tool-assisted foraging when compared to other foraging modes (Musgrave and Sanz, 2019). In Bakoun, where algae fishing becomes a highly profitable foraging strategy during the dry season, chimpanzees have never been observed to collect algae with their hands, and instead used stick tools to retrieve the algae in all instances (Boesch et al., 2017). This preference for tool use has been proposed to increase the yield of algae consumption—as deeper sections of water bodies contain more algae—while at the same time reducing the associated costs (e.g., thermoregulation) by eliminating the need for immersion in the water (Boesch et al., 2017).

Furthermore, intentional aquatic resource exploitation can involve complex decision-making strategies such as evaluating what, where and when to eat in fluctuating terrestrial environments (Trapanese et al., 2019). As such, the emergence of more sophisticated aquatic foraging behaviors in primates, such as fish-eating, was suggested to involve a gradual increase in behavioral complexity over time (Russon et al., 2014). According to this hypothesis, this behavior would start with the inadvertent acquisition of fish by naïve individuals, successively progressing into opportunistic hand-catching, followed by intentional hand-catching and finally developing into tool-assisted fish acquisition (Stewart, 2010). This hypothesis is supported by a study on fish-eating by orangutan populations in Borneo, where fish-catching that involved tool use was preceded by all hypothesized precursors (Russon et al., 2014). Comparatively, for early hominins inhabiting the coast, intertidal zones would provide a richness of edible seaweed, shellfish and fish, which when combined with other resources that wash up on the shore, such as carcasses, would provide an ideal scenario for opportunistic scavenging without the need for advanced technology (Erlandson, 2017). Over time, such practice would open up possibilities for the development of more complex and efficient strategies for foraging on marine resources. This scenario would not only be consistent with Stewart's (2010) hypothesis, but also resemble previously proposed ways in which terrestrial hunting could have developed in early hominins, beginning with confrontational scavenging, progressing toward cooperative exhaustion pursuits and ultimately leading to more complex hunting strategies involving long-distance weapons and other tools (Garcia et al., 2021). However, the scarcity of available research on the evolution of the techniques that primates use to exploit aquatic resources indicates that the existence of such a generalized pathway toward the development of this behavior remains speculative (Russon et al., 2014). In addition, different populations and species may also acquire aquatic fauna exploitation behavior through distinct pathways according to variations in local ecological conditions and required techniques (Russon et al., 2014). In this sense, it is also likely that human populations inhabiting different ecosystems started to exploit aquatic resources through distinct behavioral pathways, whether that included the consumption of fish or not.

Within this framework, when trying to infer intentionality in early hominin aquatic resource use, scientists cannot rely on direct observation, and instead must use indirect proxies. The difficulties associated with this methodology are manifold. Firstly, not all types of aquatic resource exploitation produces remains that may become material evidence, such as the consumption of aquatic flora without the use of tools. Secondly, even when tools are used, they may be made from soft material, such as those used by some non-human primates to catch algae (e.g., Matsuzawa, 1996; Boesch et al., 2017). As such, their remains are unlikely to be preserved in the archeological record, which in turn may create a bias in the material evidence preventing the accurate reconstruction of the emergence of aquatic resource exploitation in primates and extinct hominins (McGrew, 2010). In this context, most of the available evidence for aquatic foraging in early hominins comes from taphonomic analyses, frequently from sites where paleoanthropological remains are associated with aquatic fauna remains (Will et al., 2019). The use of this methodology has allowed scientists to suggest that Plio-Pleistocene hominins were exploiting aquatic resources as early as 1.95 Ma at the Turkana Basin (Archer et al., 2014). In addition, it also provided evidence for shellfish foraging and for shell tool manufacturing by *Homo erectus* in Java around 0.5 Ma (Joordens et al., 2015). Nevertheless, reliably determining whether this type of exploitation was opportunistic or not solely from faunal assemblages can be challenging, and scientists must also rely on complementary research methods that allow for dietary reconstruction, such as isotopic analyses (e.g., Lewis and Sealy, 2018). In the Neanderthal site of Vanguard cave, in Gibraltar, for example, while the taphonomic evidence points to the collection, processing and consumption of aquatic resources during the Middle Paleolithic, the absence of isotopic evidence for this behavior—as well as the absence of associated tools—suggests that this practice was opportunistic (Stringer et al., 2008; Richards and Trinkaus, 2009; McLeod, 2018). A variety of other sites provide evidence for the consumption of aquatic animals by Neanderthals in France (Hardy and Moncel, 2011), Greece, Italy, Portugal, Spain (Cortés-Sánchez et al., 2011) and Belgium (Guillaud et al., 2021), albeit without isotopic or tool-related evidence for intentional exploitation. The majority of the evidence for intentional and intensive exploitation of aquatic resources within hominins comes from Anatomically Modern Humans (AMHs), with the first record of tool-associated mollusk exploitation dating back to around 164 ka from Pinnacle Point, South Africa (Marean et al., 2007). Despite the existence of some described fishing tools from the upper Paleolithic (e.g., Gramsch et al., 2013), most lithic evidence for tool-associated fishing comes from much later during the Mesolithic (Cleyet-Merle, 1990). In this context, isotopic analyses of AMH remains also point toward a greater reliance on aquatic resources when compared with Neanderthals during the Paleolithic, albeit with significant regional variation (Richards and Trinkaus, 2009).

However, the period in which extinct hominins and modern humans may have started to intentionally forage for aquatic resources is likely underestimated for two reasons. Firstly, the post-glacial sea level rise during the Holocene has likely limited the archeological record from coastal hominin occupations from the Pleistocene (Bailey et al., 2007; Erlandson, 2017), potentially resulting in a significant loss in evidence of early coastal—and consequently aquatic—resource exploitation. Secondly, not all behaviors associated with intentional aquatic resource exploitation require technological assistance, as it is evidenced by data collected from non-human primates (Russon et al., 2014) and from ethnographical studies in modern indigenous populations consuming similar resources (Stewart, 1994). In this sense, earlier, less complex aquatic foraging behaviors could be absent from the archeological record due to lack of material remains (e.g., tools). As such, while the usage of taphonomic, lithic and observational data has promoted significant advances in our knowledge about the intentional use of aquatic resource in non-human primates and hominins, further empirical evidence is needed (1) to better detect intentionality in the use of aquatic resources in non-human primates, (2) to reconstruct the technological patterns of the emergence of this behavior, (3) to determine which early Pleistocene hominins intentionally exploited aquatic resources and finally (4) to allow for comparisons between the aquatic resource consumption patterns of non-human primates and hominins.

AQUATIC FOODS AND HOMININ BRAIN SIZE

Coastal, riverine and lacustrine ecosystems are complex and fluctuating environments, in which the availability of resources may be affected by tidal regimes, weather and seasonality. Thus, as is the case in other environments with rapidly changing conditions, primates inhabiting such areas are likely to mobilize cognitive skills that reflect a high level of behavioral flexibility in their foraging decisions (Trapanese et al., 2019; Garcia et al., 2021). In this sense, foraging in aquatic environments could imply a diversity of behavioral responses ranging from simple reflexes to more complex mental representations of goals, their values and the potential courses of action required to make decisions and optimize energetic balance in a social context. At the cognitive level, these decision-making processes are based on a set of skills—for example, episodic memory, planning and value-based decision making—which allow individuals to optimize the outcomes of their actions both at the individual and collective levels (Garcia et al., 2021). Considering the putative benefits of the consumption of aquatic foods for brain development and function (Joordens et al., 2014; Hohmann et al., 2019), many authors have proposed a potential link between the exploitation of these food sources and the evolution of brain size and cognition in hominins (e.g., Marean et al., 2007; Archer et al., 2014; Russon et al., 2014; Will et al., 2019).

In this context, while there is an overlap between the onset of aquatic resource exploitation and an increase in hominin encephalization (Braun et al., 2010; Joordens et al., 2014), it seems unlikely that the former would have triggered the latter for a variety of reasons. Firstly, intensive use of aquatic resources does not necessarily depend on high technological prowess (Carlson and Kingston, 2007; Cunnane et al., 2007; Archer et al., 2014; Russon et al., 2014). As such, the extent to which an increase in reliance on aquatic foraging behavior would generate selective advantages for larger brains remains unclear. Early hominins such as *Ardipithecus* and some species of *Australopithecus.* would have likely lived in similar habitats as chimpanzees, the latter being known to exploit aquatic resources in forested environments (Koops et al., 2019). Considering the similarities in brain size between early hominins and chimpanzees (Klein, 2009; Carlson et al., 2011), as well as similarities between the dietary needs of chimpanzees and humans for some brain-selective nutrients (e.g., iodine; Mano et al., 1987), it is possible to hypothesize that these early hominins may have also exploited aquatic resources (Koops et al., 2019), albeit without the onset of the brain expansion process observed only in later hominins. However, this hypothesis strongly relies on nutritional data, and the knowledge about which ecological conditions can contribute to the onset of aquatic resource exploitation remains scarce (Koops et al., 2019). Secondly, the pattern observed in aquatic foraging non-human primates is that of the adaptation of previous terrestrial foraging tool-use behavior and skills into aquatic foraging (Shumaker et al., 2011; Russon et al., 2014). Indeed, by the time when the first evidence for intensive aquatic resource use in hominins is recognized (ca. 1.95 Ma; Braun et al., 2010; Archer et al., 2014), hominins had already been making and using stone-tools for over a million years (McPherron et al., 2010; Harmand et al., 2015). Comparatively, by the time that the first evidence for tool-assisted aquatic resource exploitation appears in the archeological record of AMHs (ca. 164 ka in South Africa; Marean et al., 2007), Neanderthals and AMHs had already been engaging in complex forms of social hunting for over 100 ka (ca. 300 ka in Europe, Conard et al., 2020; and between 259 and 125 ka in South Africa, Bamford and Henderson, 2003). Carrying out these hunting practices, in turn, would depend on complex planning skills associated with the manufacturing of tools (e.g., wooden spears), and involving a variety of cognitive mechanisms such as working memory, context-specific goal value representations and the computation of trade-offs associated with costs and benefits (Garcia et al., 2021). In this sense, the onset of aquatic resource exploitation would not necessarily trigger an increase in cognitive complexity and brain size, as it may instead derive from the behavioral plasticity associated with already existing cognitive skills, expressed in a process of adaptive decision-making. Accordingly, we suggest that the emergence of aquatic resource use *per se*, as well as the onset of tool-assisted aquatic resource exploitation can be more parsimoniously explained as the product of a local shift in foraging cost/benefit trade-offs favoring aquatic over terrestrial resources, followed by a behavioral adaptation that optimized energetic and nutritional balance in this novel ecological context. This shift in cost-benefit trade-offs, in turn, could have been induced by a variety of locally specific factors, such as (i) seasonality (e.g., aquatic foods as fallback resources; Stewart, 2010; Archer et al., 2014), (ii) technological advancement (e.g., the repurposing of previously used skills and tools; Shumaker et al., 2011; Russon et al., 2014), (iii) physiological changes (e.g., bigger brains requiring more efficient energetic intake and more brain-selective nutrients; Navarrete et al., 2011; Potts, 2011; Joordens et al., 2014; Hohmann et al., 2019), and (iv) demographic conditions (e.g., higher benefits of aquatic resource exploitation for females and immature individuals; Koops et al., 2019).

Moreover, when considering the spatial, technological and demographic specificity of the emergence of aquatic foraging behavior in some of our closest non-human relatives (Russon et al., 2014), any overarching explanation seeking to causally link the local emergence of such behavior with a subsequent sharp development of the global cognitive abilities and brain expansion of a species seems implausible. Likewise, Joordens et al. (2014)

rule out the possibility of a driving role of aquatic resource consumption on the expansion of the human brain. According to these authors, if the early evolution of larger brains in *Homo* was driven by aquatic resource exploitation, we would expect to see a similar pattern in the context of other species that shifted toward foraging for these resources. In this context, while there is evidence that, in some animal groups, aquatic foraging species have the largest absolute brain size (e.g., herpestids, mustelids, and procyonids; Shabel, 2010), and that a shift toward aquatic foraging in cetaceans is linked to brain expansion (Marino, 2007; Xu et al., 2012), the magnitude of these associations is not comparable to the increase in brain size and cognition complexity as seen in hominins, and as such more factors are needed to explain this evolutionary transition (Joordens et al., 2014). In addition, the association between aquatic foraging and brain size does not seem hold true within non-human primate groups either, where the brains of some species that forage intensively for aquatic resources (e.g., long-tailed macaques; Tan et al., 2015) are not enlarged when compared with those of other closely related terrestrial foraging species (Navarrete et al., 2018).

Nevertheless, the exploitation of aquatic resources could have had an important role as a facilitator in the evolution of brain size and complex cognition in hominins, potentially providing a crucial fuel for our encephalization when combined with the consumption of meat (Kyriacou, 2017; Hohmann et al., 2019). Indeed, studies on human nutritional requirements provide evidence that even the consumption of a small amount of aquatic fauna could provide enough LC-PUFAs and other brain-essential micronutrients to meet daily nutritional needs of hominins (Kyriacou et al., 2014, 2016). In this sense, some researchers have hypothesized that the evolution of enlarged fat deposits in humans, for example, could be linked with an increase in aquatic resource exploitation, with adipose tissue providing an efficient way to store a surplus of consumed LC-PUFAs, and as such serving as a buffer ensuring a steady supply of brain-essential nutrients in fluctuating environments (Joordens et al., 2014). This buffering effect, in turn, could have been essential to guarantee proper cognitive function in a large part of the population during food shortage events, and particularly for individuals with decreased access to game meat, such as females and developing immature individuals (Koops et al., 2019; Will et al., 2019; Lombard and Kyriacou, 2020). As such, aquatic resource exploitation could bring about both proximate (e.g., nutritional and energetic) and ultimate (e.g., increased survival and fecundity) adaptive benefits, potentially conferring individuals or groups of individuals that engage in this behavior a selective advantage (Will et al., 2019).

In non-human primates, however, such innovative behaviors are more likely to be lost over time, either through a cessation in the display of an innovative behavior by an innovator or through the direct loss of innovator individuals (Perry et al., 2003; Nishida et al., 2009; Russon et al., 2014). Indeed, data from recent studies in captive primates suggested that besides social learning, individual learning may also influence the appearance of some behaviors such as tool-use (Bandini and Tennie, 2017, 2018, 2019; Bandini et al., 2021). Notably, in the context of aquatic foraging, Bandini and Tennie (2017) demonstrated that captive naïve chimpanzees can independently express algae-scooping behavior if provided with the necessary materials without any social learning involved. These results also suggested that while tested naïve individuals had the inherent cognitive skills to engage in algae-scooping, the emergence of such behavior was dependent on a transition to a new environmental context in which the motivation for them to do so was present (Bandini and Tennie, 2017). Thus, while there is evidence that aquatic exploitation behaviors *can* be socially learned in the wild (Russon et al., 2014; Tan, 2017), this does not necessarily mean that they *will be* socially learned, and neither that innovative behaviors will be successfully transmitted across generations and become local traditions.

As such, we hypothesize that observed disparities in the complexity and intensity with which humans and non-human primates exploit aquatic resources may have largely emerged from our increased capacity for retention and improvement of innovations over time through cultural transmission. In this sense, by increasing our dietary breadth and by fueling population growth through increased survival and fecundity (Will et al., 2019), the emergence and intensification of aquatic foraging behavior in hominins could have broadened the diversity of social and environmental contexts to which hominins would have to apply their decision-making skills. In turn, this process would have created novel cognitive challenges requiring more effective decision-making in these more complex ecological contexts. Therefore, while the exploitation of aquatic resources may not have triggered the onset of hominin brain expansion, it could have contributed to an intensification of the selection for more advanced global cognitive skills translated into larger brains. These larger brains, in turn, would require an increase in energetic intake (Navarrete et al., 2011; Potts, 2011), and especially of brain-selective nutrients, which tend to be abundant in aquatic foods (Joordens et al., 2014; Hohmann et al., 2019). As such, this process could then lead to a shift in the cost/benefit ratio of foraging on aquatic foods by increasing the payoff of this activity. In this context, given the strategic and non-random nature of social learning, this increase in payoff would selectively favor the social spread of innovations that optimize aquatic resource exploitation (Laland, 2004; Rendell et al., 2011; Whitehead et al., 2019). Additionally, this could have also influenced the selection for physiological traits that allow for better storage of important brain nutrients such as LC-PUFAs (Joordens et al., 2014). Finally, in areas where aquatic resources are abundant and diverse, these adaptations could fuel additional stable population growth and promote further expansion in the cultural repertoire of hominins (Kolodny et al., 2016; Will et al., 2019). Markedly, this adaptive scenario would only be possible if behavioral innovations associated to the optimization of aquatic resource exploitation could be successfully transmitted between individuals and across generations, which would depend on positive selection for traits that increase reliance on social learning and culture in such populations. This interpretation is consistent with studies suggesting a link between coastal adaptation and selective pressures for prosociality in hominins (Marean, 2014, 2016) and also with evidence from modeling research demonstrating that even small-scale population growth can lead to disproportional effects on cultural accumulation through a positive feedback loop process (Creanza et al., 2017). Still, in order to verify whether the relationship between aquatic resource exploitation, cognition and brain expansion in hominins constitutes an example of gene-culture coevolution, further empirical evidence is needed.

IMPLICATIONS FOR HOMININ SPATIAL ECOLOGY

While a variety of cultural behaviors has been documented in non-human primate species (Whiten, 2011; Whiten and van de Waal, 2017), the extent to which humans are able to accumulate and disseminate cultural changes over generations is unmatched (Mesoudi and Thornton, 2018). This increased capacity for cumulative cultural evolution is thought to have allowed hominins to inhabit a wide range of ecosystems, making use of a remarkable diversity of survival tools and techniques developed over time (Boyd and Richerson, 1996). As such, the extent to which hominins have been able to adapt to inhabiting coastal landscapes is unparalleled among primates, albeit there are examples of secondary adaptations to aquatic lifestyles in a variety of vertebrate species (Mazin and de Buffrénil, 2001; Houssaye and Fish, 2016; Davis, 2019). In this sense, coastally adapted populations exhibit a set of behavioral traits which allowed them to strategically occupy coastal and near-coastal zones in settlement systems with reduced mobility, and where the systematic consumption of marine resources would take place in accordance with tidal regimes and fluctuating food availability (Marean, 2014; Will et al., 2019). Thus, true coastal adaptation would not only involve the habitual consumption of aquatic resources, but also the incorporation of marine resources into the local material culture and the display of specialized technologies that allow for the more efficient exploitation of such resources (Will et al., 2019). Similarly, some non-human primate species that intensively exploit aquatic resources also exhibit other adaptations that are accessory to aquatic foraging, such as agile swimming in rhesus macaques (Mallick, 2019) and the intensification of percussive tool use in bearded capuchins (Santos et al., 2019b). As such, the success of primates—hominins included—in colonizing flooded habitats seems to depend on their capacity to efficiently exploit aquatic resources, which likely involves a variety of complementary adaptations.

In this context, a growth in the effectiveness of coastal resource extraction combined with an increase in sedentism can cause the depletion rate of some high-quality marine food stocks to accelerate. At coastal archeological sites in South Africa, for example, there is evidence for a decline in shellfish size from middle (MSA; ∼120–60 ka) to the late stone age (LSA; ∼12–1 ka) deposits, presumably as a result of hominin impact (Klein and Steele, 2013). A decrease in limpet size associated to late Neanderthal exploitation has also been documented during the Upper Paleolithic (UP) in Europe, which may potentially be associated to increases in population growth and density during that period (Stiner et al., 1999). In addition, modeling research on cultural evolution shows that, through changing resource availability, technological development may result in further population growth (Kolodny et al., 2016), which in turn could expedite the reduction in the local availability of high-quality marine foods (Klein et al., 2004; Niespolo et al., 2021). In this context, a decrease in size and quality of marine stocks could cause a reduction in the yield, and consequently also in the benefit of foraging on local aquatic resources. Moreover, higher population sizes and densities would also generate an increase in intraspecific competition for such resources, raising the costs and risks associated to acquiring them. In response to a shift in the cost-benefit relation of foraging in marine foods, populations would have two ways in which to flexibly adapt: (i) through further technological development that would increase food access (e.g., shifting toward the consumption of more agile, harder-to-catch prey; Stiner et al., 1999) or (ii) through territorial expansion or migration to other inland or coastal areas (e.g., Walter et al., 2000).

Indeed, it has been proposed that some of the earlier terrestrial hominin dispersals out of Africa and into Eurasia have been influenced by food availability and facilitated by similarities in access to resources across sites without predetermination (Prat, 2018). Comparatively, a similar process could have pushed for hominin dispersal along the coast and through the sea. This is specially the case considering similarities in resource availability between some coastal zones, and the presence of intricate oceanic current systems in areas with higher density of islands which may further facilitate dispersal (Erlandson, 2017). In this sense, this facilitation may have been crucial to the success of such hominin dispersals, especially considering that water bodies often also represent substantial biogeographic barriers in the context of non-human primate spatial ecology (e.g., Harcourt and Wood, 2012; Boubli et al., 2015; Shekelle et al., 2019). Notably, a variety of authors has proposed the existence of migration corridors along coastal zones which would likely not constitute substantial ecological barriers for oceanic movement, e.g., the kelp highway along the Pacific Rim (Erlandson et al., 2007, 2015) and the mangrove rim along the Indian Ocean (Kathiresan and Rajendran, 2005). Therefore, dispersals along such coastal migration corridors could have been associated with low technological costs and reduced failure risks, particularly for populations with a high degree of adaptedness to a coastal lifestyle.

Accordingly, a scenario of progressive colonization of different coastal ecosystems could have pushed hominins to display adaptive behaviors in response to novel subsistence challenges and opportunities, likely involving the cultural accumulation and diversification of novel technologies used to exploit aquatic resources and of technologies necessary for water crossings (Gaffney, 2021). Incrementally, this could culminate in the development of maritime adaptations by some human populations, involving intensive use of boats and other sea-going vessels, off-shore exploitation of marine resources and more frequent long-distance sea traveling (Will et al., 2019). Within this framework, an increase in complexity of coastal occupations and water crossings would also impose novel relevant cognitive challenges to hominins (Leppard, 2015b;

Leppard and Runnels, 2017). Unlike passive dispersal, strategic longer distance water crossings would require the use of composite technologies, further capacity for projecting future actions to achieve to out-of-sight goals and an ability to engage in more complex cooperative planning interactions (Leppard, 2015a). In this sense, this process could, at least partially, account for observed differences in frequency and intensity of sea dispersals between early and late Pleistocene hominins, with the latter exhibiting higher adaptedness to coastal ecosystems and being more cognitively ready to flexibly adapt to novel environments. Together, such adaptations would also have putatively allowed populations to increase the yield of their foraging behavior and to diversify the array of readily available aquatic resources. In turn, this could confer such populations with a further adaptive advantage, allowing for the progressive increases in efficiency and spread of demographic expansions via water crossings observed in the paleoanthropological record from the Early to the Late Pleistocene (Gaffney, 2021).

GENERAL DISCUSSION AND PERSPECTIVES

Although the consumption of aquatic resources has been reported in populations of several non-human primate species (Stewart et al., 2008; Kempf, 2009; Stewart, 2010; Russon et al., 2014; Koops et al., 2019), little is currently known about the ecological conditions that favor the emergence and permanence of this behavior in some—but not all—populations that have access to aquatic resources in the wild. In part, this has to do with the lack of studies tracking the emergence of aquatic foraging behavior in a wild setting, of which Russon et al. (2014) is an exception, having documented the appearance of fish-eating behavior among ex-captive, rehabilitated orangutans in Borneo. Evidence from this study, in turn, seems to be in line with Stewart's (2010) hypothesis that the emergence of complex aquatic resource exploitation would be preceded by simpler behavioral precursors, with the transition from simpler to more complex behaviors gradually developing over time. Still, when considering the myriad of local specificities that may affect aquatic foraging behavior in non-human primates—such as local food availability (e.g., Matsuzawa, 2019), demography (e.g., Koops et al., 2019) and employed techniques (e.g., Sakamaki, 1998; Boesch et al., 2017)—any individual explanation seeking to globally explain the emergence of such behaviors is unlikely to offer a high explanatory power in a local context. Instead, future research may benefit from adopting a comparative approach for studying why non-human primates may favor aquatic over terrestrial resources in some ecological contexts, but not in others. By doing this, researchers would be able to get a better understanding of what cognitive processes may cause some non-human primate populations to transition from an entirely terrestrial diet to one that also includes aquatic foods. Besides, this approach could also aid in assessing the extent to which this transition may be favored by local cost-benefit trade-offs and how such behaviors perish or persist over time across different populations and species.

Regardless of the mechanisms behind their emergence, the presence of widespread and intensive aquatic foraging behaviors in some non-human primate populations (e.g., long-tailed macaques; Gumert et al., 2009; Gumert and Malaivijitnond, 2012; Tan et al., 2015; Tan, 2017) hints at an important role played by these items in their local foraging ecology. According to the optimal foraging theory, this should be specially the case for species that forage for aquatic resources intentionally, as their observed foraging strategies are expected to have resulted from cognitive processes that optimize the energetic balance in dynamic ecological contexts (Charnov, 1976; Stephens and Krebs, 1986). However, considering that the available evidence for intentionality in aquatic resource exploitation by non-human primates mainly comes from planning behavior related to tool selection and use, our current record of how many species consume aquatic resources intentionally likely represents an underestimation. As such, the use of other proxies (see below) to investigate intentionality in non-human primate aquatic foraging is central to future research, and particularly in the case of species that do not use tools when foraging in coastal, riverine or lacustrine environments. In the context of terrestrial foraging, for example, one method that has been proven useful for determining intentionality has been the use of a combination of movement, environmental and behavioral data to study the decision-making processes of primates in the wild on a contextual ecological basis, which in turn helps shed light on what information individuals are acting on and what cognitive skills are associated with their observed behaviors (e.g., Janmaat et al., 2014; Ban et al., 2016; Salmi et al., 2020; but see Janmaat et al., 2021 for a review of this method). By applying such novel methods, researchers could be able to determine, for example, whether the aquatic foraging behavior of coastal-dwelling primates are part of a plan (e.g., if they schedule their foraging to tides) or how the seasonal availability of different aquatic resources spatiotemporally affects their behavior. In addition, this could also allow for determining whether aquatic foods may truly be preferred to terrestrial ones on some environmental contexts, or whether they may simply represent fallback resources in times of terrestrial food shortages.

Moreover, with hominins being the only primate group in which true coastal adaptation has evolved (Will et al., 2019)—and consequently also the one in which the most intensive and complex exploitation of aquatic resources can be observed—such diversification in methodologies could be crucial for a better appraisal of currently existing hypotheses on how the consumption of aquatic resources may be linked to the evolution of the hominin brain and cognitive skills. Additionally, in light of the putative cultural nature of coastal adaptation in hominins (Marean, 2014; Will et al., 2019), future studies could also benefit from assessing foraging decision-making processes at the collective level and the social transmission of behaviors between individuals as an important factor influencing the development of aquatic foraging in extinct hominins. This approach would be of particular value when considering the patterns of aquatic resource exploitation in AMHs, as our species is not only the one for which the largest body of evidence for coastal adaptedness is available, but also the only one in which advanced maritime adaptations have been detected

(Erlandson, 2001, 2017; O'Connor et al., 2011; Fujita et al., 2016)—the latter likely being unique in the complexity of cognitive skills and collective decision-making efforts required to achieve it (Leppard, 2015a,b; Leppard and Runnels, 2017). That said, the relatively lower amount of evidence for a high degree of coastal and maritime adaptedness in other hominin species (e.g., Neanderthals and *Homo erectus*) may also be a product of the loss of coastal archeological remains of such hominins due to the post-glacial sea level rises during the Holocene (Bailey et al., 2007; Erlandson, 2017). Finally, an important knowledge gap remains with respect to how the exploitation of aquatic resources in hominins may have been linked to the regular use of fire and cooking. Given the centrality of cooking in the evolutionary context of hominin foraging ecology (Carmody and Wrangham, 2009), the association between this activity and aquatic foraging becomes specially important when considering that the detection of widespread regular use of fire in the paleoanthropological record (ca. 400–350 ka) predates the earliest available evidence for the appearance of intensive aquatic resource exploitation in AMHs—ca. 164 ka—by over 150,000 years (Marean et al., 2007; MacDonald et al., 2021). Nevertheless, accurate detection of burning traces on aquatic fauna remains can be a challenging and inconclusive process (Guillaud et al., 2021), and more evidence is still needed in order to better assess when hominins first started cooking aquatic foods.

In summary, by adaptively responding to novel ecological challenges linked to local changes in foraging cost-benefit trade-offs, hominin populations have been able to strategically expand their niches through diversifying their diets to include a wide variety of aquatic resources. Over time, the intensification of aquatic resource exploitation combined with higher sedentism and population growth may have led to the development of long-lasting coastal adaptations in AMHs, later followed by maritime adaptations involving advanced sea-faring technologies and deliberate water crossings toward new geographical regions (Erlandson, 2017; Will et al., 2019). Markedly, these ecological shifts were likely linked to key cognitive skills in hominins allowing for a higher level of adaptive flexibility (Leppard, 2015b), which when combined with an increased capacity for accumulating cultural changes over time (Mesoudi and Thornton, 2018), may have translated into an unmatched readiness to adapt to novel ecological niches (Boyd and Richerson, 1996; Wright et al., 2010; Gaffney, 2021). Thus, it is clear that the unique ways in which some coastal populations have been able to exploit aquatic resources most likely had a deep impact on the ecological trajectory of hominins. In this sense, developing a better comparative understanding of how such behavior can emerge in hominins and non-human primates may have profound implications for how we interpret hominin evolution.

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CG and SP provided the initial ideas for this review. GC wrote the body of the manuscript. All authors have participated in the writing, conception and discussion of ideas presented in the final version of this review.

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Dietary Choices of a Foregut-Fermenting Primate, *Colobus guereza*: A Comprehensive Approach Including Leaf Chemical and Mechanical Properties, Digestibility and Abundance

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Free-ranging animals make dietary choices that affect their nutritional status and, ultimately, their health and fitness. We investigated food selection by a leaf-eating foregut-fermenting primate, the guereza (*Colobus guereza*), using multiple criteria, including chemical and mechanical properties, *in vitro* digestibility and leaf abundance, on the basis of 30 consecutive months of behavioral observations (4308 h in total) of a family group in the Kalinzu Forest, Uganda, as well as vegetation surveys. We noted that leaf toughness may be a proximate cue for the chemical properties of plant foods, especially for protein, which is an important selection factor used by primates. We also found that the *in vitro* digestibility of plant foods was greatly influenced by the concentrations of fiber and secondary compounds. At a broad level, none of the studied factors, including leaf chemical and mechanical properties, digestibility and abundance, affected whether guerezas consumed specific leaf items. At a more detailed level, however, protein content, digestibility and toughness were related to the percentage of foraging effort that guerezas devoted to specific items in our study site.

Keywords: feeding ecology, folivore, food mechanical properties, nutritional ecology, secondary compounds

INTRODUCTION

Tropical forests offer herbivores a variety of potential food sources. Therefore, to meet their nutritional needs and maintain their health and fitness, herbivores must select foods on the basis of criteria such as their chemical and mechanical properties, weighed against the availability of food resources. Since the variety of plant species eaten by herbivores may vary substantially in terms of nutritional content, toughness, secondary compounds, abundance, and digestibility (Janzen, 1973; Crawley, 1983; Onoda et al., 2011), many studies have reported some degree of herbivore food selectivity (Hughes, 1990; Cassini, 1994; Iason and Villalba, 2006). Thus, over the past half century, a considerable amount of knowledge has accumulated with respect to the dietary choices of herbivores, though the same species have often been found to use different dietary choice criteria under different environmental conditions (Cassini, 1994; Ganzhorn et al., 2017); this suggests that further empirical research that evaluates this flexibility is worthwhile.

Foregut-fermenting primates, the colobines, are a group of Afroeurasian monkeys that include over 70 species that are widely distributed throughout Asia and Africa. Their foregut fermentation system features a multi-chambered stomach where a commensal microbiome digests plant cell walls and can detoxify defensive plant chemicals (Chivers, 1994; Matsuda et al., 2022). This fermentation system enables these primates to exploit a diet of leaves in great quantities (Fashing, 2011; Kirkpatrick, 2011). As in many herbivorous mammals (Gordon and Prins, 2019), nutritional studies of colobines have revealed that they generally prefer foods containing more protein and less fiber (Waterman and Kool, 1994; Rothman et al., 2022). However, some colobines do not exhibit a strong preference for protein; in fact, a clear preference for protein is generally only seen in environments with low average protein content (Oftedal, 1991; Ganzhorn et al., 2017; Evans et al., 2021). Additionally, since leaves typically contain many plant secondary metabolites, it is hypothesized that colobines have strategies to detoxify, tolerate or avoid these compounds. Several studies have reported food choices that avoid tannins and/or alkaloids (Oates et al., 1977; Oates, 1988; Fashing et al., 2007). Conversely, there are also reports of a lack of active avoidance of secondary compounds (Davies et al., 1988; Mowry et al., 1996; Huang et al., 2010; Liu et al., 2013; Matsuda et al., 2013). Thus, the combined effects of food chemical properties and other possible factors such as digestibility, toughness and food abundance must be considered to understand the dietary choices of colobines. However, to our knowledge, little is known about the dietary choices of colobines with respect to a larger variety of factors, particularly when they are presented simultaneously.

In addition to chemical properties, variation in the mechanical properties of food plants is believed to influence primate feeding behavior in relation to the morphology of their dentofacial complex (e.g., Lucas and Teaford, 1994; Koyabu and Endo, 2009; Wright and Willis, 2022) and hence their food selection (e.g., Dominy et al., 2001; Huang et al., 2010; Matsuda et al., 2017); in other words, they typically select tender foods. Additionally, in leaf-eating colobines, the selection of leaves with a low degree of toughness may be an adaptive strategy as ingestion rates are negatively correlated, and masticatory investment is positively correlated, with leaf toughness (Dunham and Lambert, 2016). Furthermore, toughness, as assessed by oral sensation, may serve as a proximate cue of the food's chemical properties, as it depends on the concentration of fiber, such as cellulose, hemicellulose and lignin (Lucas et al., 1997; Dominy et al., 2001). Protein content also has a negative relationship with the toughness of food sources consumed by Asian colobines (Matsuda et al., 2017), supporting the fact that leaf toughness is used as an important cue to evaluate nutritional quality.

Assessing digestibility can be an optimal way to comprehensively quantify food quality as represented by multivariate chemical and physical factors and has been done using *in vitro* assays. Although some previous studies have used assays combining acid and enzymatic treatments (e.g., Oates et al., 1980; Choo et al., 1981), live gut microbes contained in fresh feces are often used as inoculum, with a specific food as a substrate (e.g., Campbell et al., 2002; Schmidt et al., 2005; Hanya et al., 2020). Recent molecular studies have shown that bacterial communities diverge between the foregut and hindgut in colobines (Clayton et al., 2019), with the higher expression of microbial gene functions for fiber digestion in the foregut than in the hindgut (Liu et al., 2022); thus, feces that contain hindgut-derived microorganisms may not be a representative inoculum source for measuring digestibility in foregut-fermenting colobines. Although limited information is available on the foregut microbial community in colobines (Zhou et al., 2014; Amato et al., 2016; Hayakawa et al., 2018), it should not deviate substantially from that of other foregut-fermenting animals such as artiodactyls (Matsuda and Clauss, 2022), indicating that the most common *in vitro* method for measuring digestibility in herbivores, using a standardized inoculum and domestic ruminant rumen fluid [e.g., the modified Hohenheim gas test; (Menke et al., 1979)], should also be applicable for foregut-fermenting colobines (Waterman et al., 1980; Chapman and Chapman, 2002; Chapman et al., 2004; Matsuda et al., 2017).

Finally, optimal dietary choices should also depend on energy values, as well as handling and search times (Davies et al., 2012). Hence, it is important to consider the availability of foods and their heterogeneous distribution within forests (Boinski and Garber, 2000). Even in colobines, whose primary food source is leaves, which appear to be ubiquitous and abundant, leaf availability may explain diet selection (e.g., Chapman and Chapman, 2002; Hanya and Bernard, 2012; Matsuda et al., 2017), although some species do not base their diet simply on abundance (Zhou et al., 2006, 2013).

Black-and-white colobuses, or guerezas (*Colobus guereza*), are widely distributed throughout Africa (Fashing, 2022) and generally form small groups, typically averaging 7–11 individuals including one or two adult males, several adult females and immatures (Fashing, 2022). They have been reported to have considerable intraspecific variability in their diets, both over time and space, ranging from highly folivorous to including large quantities of fruit (Fashing, 2022). As for their dietary choices, protein content is one of the primary indicators in their decision to eat a particular leaf (Chapman et al., 2004; Fashing et al., 2007). Conversely, protein content and/or protein-to-fiber ratios are also positively correlated with the leaf foraging efforts of guerezas in Kibale, Uganda (Chapman et al., 2004), whereas in Kakamega, Kenya, they consume leaves on the basis of fiber, but not protein content (Fashing et al., 2007). Only one study (Chapman et al., 2004) has reported leaf digestibility as a considerable factor in dietary choice: depending on the forest environment (i.e., unlogged or fragmented forests), there is a marked difference between leaf selectivity and digestibility. Conversely, no studies have completed a comprehensive assessment of guereza leaf selectivity, including leaf toughness.

Here using a comprehensive dataset, we examined the relationship between a number of factors (i.e., leaf chemical and mechanical properties, *in vitro* digestibility, toughness and abundance) and food choice in a guereza population in Kalinzu Forest, Uganda, to establish the factors that are the most relevant proxies for guereza diet selection. First, we examined the relationship between leaf toughness and the chemical properties of the leaves in order to understand the functional traits of the leaves collected in the study site, including those consumed by the guerezas. As in earlier studies reviewed above (Lucas et al., 1997; Dominy et al., 2001; Matsuda et al., 2017), we predicted that leaf toughness would be positively correlated with fiber content, but negatively correlated with protein content. Second, to understand the general pattern of *in vitro* digestibility in relation to chemical properties of leaves, we also examined the respective relationships. We expected that fiber and secondary compounds would have negative effects on *in vitro* digestibility (Choo et al., 1981). Third, we compared the multivariate chemical, physical factors and digestibility of leaves eaten and not eaten by the guerezas. We predicted that guerezas would preferentially feed on leaves with lower toughness and higher digestibility than common plant species, rather than just those with higher protein and lower fiber levels (or higher protein: fiber ratio) often demonstrated in dietary choice models of folivorous primates (e.g., Milton, 1979). Fourth, we examined the selectivity within the plant species on which guerezas consumed. Referring to a study in another colobine species which considered multiple factors (Matsuda et al., 2017), we predicted that, apart from nutritionally, mechanically and digestibility advantageous diets, selectivity within the plant species consumed by guerezas would most likely indicate that they choose leaf species that were abundant at the study site. Therefore, in screening whether to eat or not to eat, we expected that food selection by guerezas would take into account nutritional, ingestion and digestive efficiency, but that selectivity within the plant species eaten would prioritize the optimal foraging strategy, i.e., saving travel costs when searching for foods. In our analysis of this comprehensive dataset, we sought to establish the measures that might be the most relevant proxies of dietary choice by guerezas at the study site.

MATERIALS AND METHODS

Study Site and Collection of Behavioral Data

We conducted our study in a moist, medium-altitude evergreen forest in the Kalinzu Forest, western Uganda, covering an area of 137 km^2 [30°07’ E, 0°17’ S; altitude 1000–1500 m above sea level; (Hashimoto et al., 1999)]. Mean minimum and maximum temperatures were approximately 14 and 27°C, respectively, and the total annual precipitation at the site was 1370 mm (Matsuda et al., 2020).

From November 2011 to October 2012, preliminary observations were conducted on several guereza groups before the most habituated group was chosen for the study. During these preliminary observations, members of a focal group were identified by describing their individual physical characteristics. Thus, we successfully followed a well-habituated, identifiable group that included 11 individual guerezas at the end of the preliminary observation period: one alpha male, three adult females, two subadult females, two juveniles and three infants (Matsuda et al., 2020).

From November 2013 to April 2016, behavioral observations were conducted for 10–22 days/month from approximately 7:30 to 16:00 (8.00 ± SD 1.01 observation hours per day and 4,308 h in total) using scan sampling at 10 min intervals. We recorded the activity (feeding, moving, and resting) of all visible adults and subadults ranging from one to seven individuals with a mean number of 4.8 ± SD 1.2 individuals per scan. We recorded the food category and collected samples for later identification when they were feeding (Matsuda et al., 2020). Continuous observations permitted the calculation of time budgets for the adult and subadult monkeys, such as the proportion of the day spent feeding and the time spent feeding on individual food items. Overall, the studied guerezas devoted 87.0% of their feeding time toward young leaves, 9.8% to fruits, 1.1% to flowers, 0.9% to bark, 0.8% to soil and 0.4% to unspecified foods and mature leaves. The numbers of plant species that provided these young leaves, fruits and flowers were 31, 12, and 6, respectively (Matsuda et al., 2020).

Vegetation Survey

On the basis of the focal group’s range data collected during preliminary observations, we selected 12 trails that were 180–900 m long (total 4700 m) within the study site. We labeled trees of $\geq$ 10 cm in diameter at breast height and vines of $\geq$5 cm in diameter located $\leq$1.5 m from the trail; hence, the labeled width was 3 m. The survey area covered 1.41 ha, including 969 trees and 27 vines from 68 species, 57 genera and 35 families (Matsuda et al., 2020). Food abundance was determined as the number of potential food plants for the guerezas.

Leaf Sampling

To compare the chemical properties, toughness and digestibility of young leaves that were both consumed and not consumed by the guerezas, leaf samples were collected in July 2014. For each plant species, young leaf samples were collected from at least four individual trees/vines in the vegetation survey area. We had planned to collect young leaves of all species that accounted for >0.1% of the feeding time (99.4% of the total feeding time) and the 20 most abundant species (defined according to the total number of plant species in the study area as assessed during the vegetation survey); however, because of the logistical difficulties of sampling leaves from treetops, samples from only 16 of the 20 most consumed species could be collected (96.9% of the total feeding time). Seven plant species also overlapped across the two categories, i.e., young leaves of all species that accounted for $>0.1\%$ of the feeding time and the 20 most abundant species in the vegetation survey. Thus, 29 plant species were evaluated in this study (i.e., 19 consumed and 10 non-consumed species).

Chemical Analysis

The plant samples collected were dried at $\leq 60°C$ immediately after collection in the field station and stored with desiccant in plastic bags for approximately 1 month. The samples were then re-dried at 60°C and milled for chemical analysis at the laboratory. Ground samples were sent to Tokachi Federation of Agricultural Cooperatives (Hokkaido, Japan) for nutrient analysis. The following nutritional components were analyzed using standard procedures (AOAC., 2012): crude protein (CP: AOAC no. 977.02), crude lipid (CL: AOAC no. 963.15), total ash (TA: AOAC no. 942.05), NDF corrected for residual ash (neutral detergent fiber expressed without residual ash: AOAC no. 2002.04). For each tree and vine species, young leaf samples were collected from at least four individual plants in or around the vegetation survey area.

Leaf Toughness

Young leaves from the collected plant species were immediately measured for toughness *via* a punch test (originally measured as kilogram-force; 1 kgf = 1 kg $\times$ 1, G = 1 kg $\times$ 9.8, 0665 m/s^2 = 9.80665 N, to convert SI units to kPa). To determine the mass needed to penetrate a leaf, a penetrometer (Kurokawa and Nakashizuka, 2008) with a 3 mm diameter column (digital force gauges: IMADA Co., Ltd., Aichi, Japan) was used. The measurement was performed on 30 leaves collected from at least four individual plants per plant species, and the results were averaged for each species.

In vitro Fermentation

All experimental methods were conducted in accordance with relevant guidelines and regulations. A modified Hohenheim gas test (Menke et al., 1979) was used in an *in vitro* fermentation system to quantify the degradability of the young leaf samples (which had previously been submitted to chemical and toughness analysis). The inoculum was obtained from the rumen fluid of cattle fed a standardized, forage-dominated diet since the inoculum typical for guerezas was not available. However, the use of a standardized inoculum source made it possible to compare the current results with the *in vitro* results from other studies. The relative abundance of microbes and their taxonomic assignments in the forestomach of colobines should be similar to those in cattle (Zhou et al., 2014; Hayakawa et al., 2018). A total of 200 mg of milled plant tissue was weighed in airtight glass syringes together with the inoculum, as described previously (Hummel et al., 2006), and incubated at 39°C for 24 h. Gas production (Gp) was recorded after 4, 8, 12, and 24 h. Gas produced during fermentation reflects the extent of food degradation; it consists of nearly equal parts of the waste gases of fermentation and the CO_2 from the buffer (bicarbonate) reaction with the volatile fatty acids produced during fermentation (Blümmel et al., 1999). Leaves were analyzed with and without 200 mg of polyethylene glycol (PEG), which was added to reduce the negative effects of tannins on digestion (Makkar et al., 1995). Samples were used for two tests on two different days (with two replicates each time). Gp at 24 h was used as the digestibility value of young leaves for guerezas. Additionally, we used the difference in digestibility with and without PEG (i.e., GP [24 h] with PEG and Gp [24 h] without PEG) as an indicator of secondary compounds such as tannin.

Data Analysis

Factors Affecting Leaf Toughness and Digestibility

To examine the relationship between leaf toughness and the chemical properties of the leaves, a linear model was used to establish whether leaf toughness in the tested plants (29 plant species) was affected by chemical factors such as NDF, CP, CL, and TA. The measured toughness value was the normally distributed response variable, and the other factors were treated as explanatory variables. To examine the relationship between *in vitro* digestibility and leaf traits, a linear model was also used to assess whether the leaf digestibility (Gp at 24 h) of all collected plants (i.e., 29 plant species) was affected by chemical properties, toughness and indicators of secondary compounds. The digestibility (with and without PEG) of young leaves was normally distributed, and the other factors were treated as explanatory variables.

Dietary Choice Between Eaten and Not Eaten Leaves

To determine the factors that may explain guerezas' leaf preferences, we employed a generalized linear model using the leaf chemical properties, toughness, abundance (number of plants found in the vegetation transects), digestibility (with and without PEG) and indicators of secondary compounds and applied binomial regression family calculations to obtain the AICc. Leaf preference (i.e., the consumed or non-consumed food types) was treated as the categorical response variable, and the other variables were treated as explanatory variables.

Dietary Choice Within Eaten Leaves

We also investigated the effects of leaf traits, abundance, digestibility and indicators of secondary compound for the consumed plant species in terms of the percentage of feeding time [as determined by Matsuda et al. (2020)] using a linear model. The proportion of time spent feeding was logit transformed [log $(p/1-p)$] and treated as a normally distributed response variable; the other factors were treated as explanatory variables.

For all models, we verified that the variance inflation factors were smaller than the cut-off value, i.e., less than 10 (Quinn and Keough, 2002); therefore, collinearity among independent factors (explanatory variables) did not affect the results. For model selection, we examined a set of models with all possible combinations of the explanatory variables and ranked them using AIC corrected for small sample sizes, i.e., AICc (Burnham and Anderson, 2002). Following the guidelines published for wildlife research, we selected the best-supported models as those with a ΔAIC(c) score ≤ 2, where ΔAIC(c) = AIC(c) $-$ minimum AIC(c) within the candidate model set (Burnham and Anderson, 2002). All analyses were conducted using R ver. 4.1.0 (R-Core-Development-Team., 2021), employing the dredge function in the MuMIn package (Barton, 2012). As our data set is based on only 11 individuals belonging to one group of guerezas, extrapolating our results to a population level remains speculative.

RESULTS

Factors Affecting Leaf Toughness and Digestibility

The best-fit model to explain leaf toughness, as evaluated using the AICc, included CP and NDF (**Table 1** and **Figures 1a,b**), although the ΔAICc value of the following models including CP, NDF, TA and indicators of secondary compounds (**Figures 1a–d**) was also <2.0; leaf toughness increased with increasing TA and decreasing CP content, NDF content and secondary compounds. Out of both model groups for digestibility with/without PEG, with ΔAICc < 2, the best-fit model included NDF and indicators of secondary compounds (**Figures 1e–h**), which had negative effects (**Table 2**). The second-best model was the null model in both cases.

Dietary Choice

Table 3 shows the properties of the consumed and non-consumed leaves. Leaf digestibility (gas production) was generally similar across the consumed and non-consumed leaves, although the consumed leaves produced slightly more gas than the non-consumed leaves, with consistent differences between the *in vitro* assays with and without PEG. Model selection for the investigation of whether guerezas choose young leaf species on the basis of their chemical properties, abundance, digestibility, indicators of secondary compounds and/or toughness, revealed that the null model was the top model. The second-best models,

TABLE 1 | Summary of model selection for linear models used to examine the effect of leaf chemical properties on leaf toughness (only models with ≤ΔAIC 2 are shown).

Intercept	Total ash	Crude lipid	NDF	Crude protein	Indicator of secondary compounds	df	Log-likelihood	AICc	Δ AICc	AICc weight
2.99			−0.02	−0.03		4	−18.2	46.1	0	0.22
2.74	0.05		−0.02	−0.04		5	−16.9	46.4	0.23	0.20
3.39			−0.01	−0.04	−0.04	5	−17.4	47.5	1.39	0.11

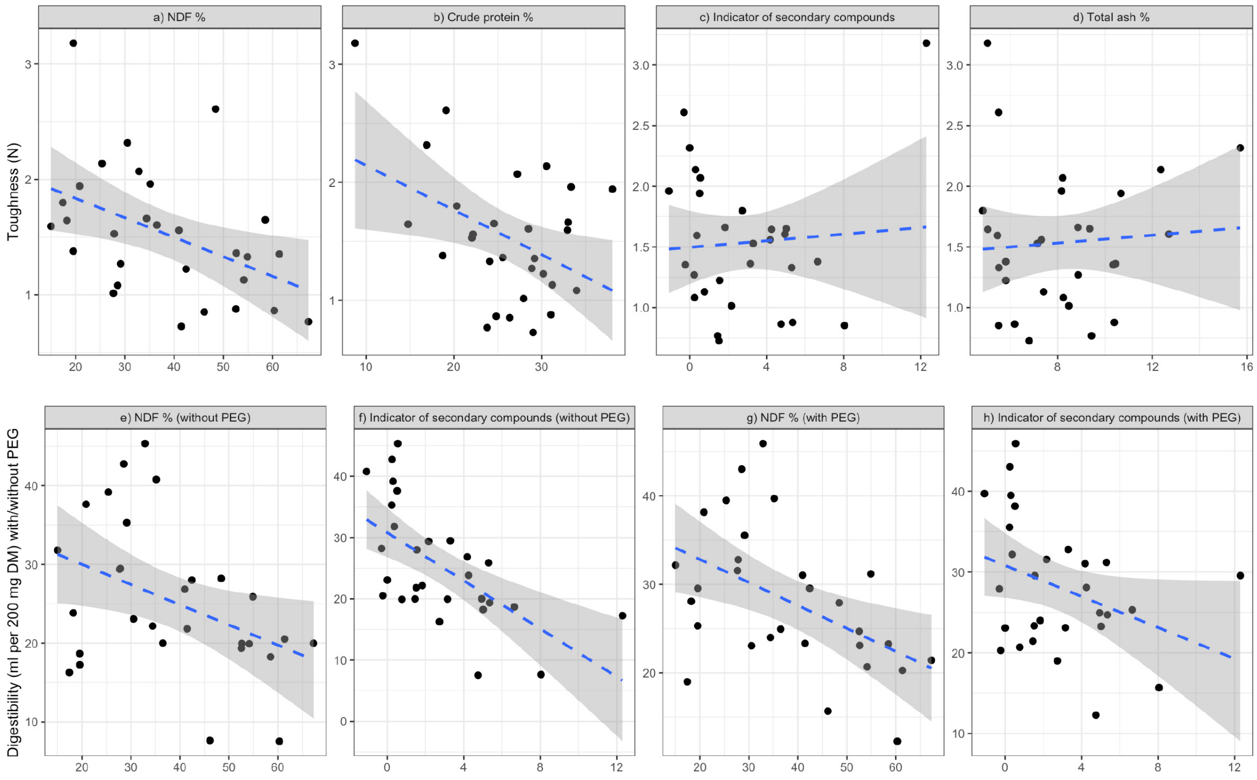

FIGURE 1 | Relationships of leaf toughness **(a–d)** and *in vitro* digestibility **(e–h)** with chemical properties, respectively, based on the model selection **Tables 1**, **2**. Blue dotted lines and shaded areas represent the linear regressions estimated by the "lm" method in R for the observed samples and their 95% confidence interval ranges, respectively.

TABLE 2 | Summary of model selection for linear models used to examine the effects of several leaf traits (e.g., chemical properties, toughness and indicators of secondary compounds) on leaf digestibility (Gp at 24 h) without PEG (A) and with PEG (B) (only models with $\leq \Delta$AIC 2 are shown).

	Intercept	Total ash	Crude lipid	NDF	Crude protein	Toughness	Indicator of secondary compounds	df	Log-likelihood	AICc	Δ AICc	AICc weight
(A)	24.21			−0.36			−2.08	4	−59.8	130.5	0	0.46
(B)	43.23			−0.36			−1.00	4	−59.845	130.5	0	0.29

TABLE 3 | Leaf traits and digestibility [mean ± standard deviation] of the young leaves from abundant trees in the study site, with respect to guereza preferences.

	Digestibility without PEG	Digestibility with PEG	Toughness	Abundance	NDF	Crude protein	Total ash	Crude lipid
	(ml per 200 mg DM)		(N)	(Number of plants in survey area)		(Proportion of dry weight)		
Non-consumed leaves (*N* = 10)	23.8 ± 6.95	26.0 ± 6.0	1.48 ± 0.50	38.3 ± 52.1	0.38 ± 0.15	0.25 ± 0.06	0.08 ± 0.03	0.02 ± 0.02
(Range)	(16.3–40.8)	(19.0–39.7)	(0.73–2.32)	(10–184)	(0.17–0.67)	(0.17–0.33)	(0.04–0.16)	(<0.01–0.06)
Consumed leaves (*N* = 22)	26.3 ± 10.7	29.3 ± 8.9	1.56 ± 0.62	22.9 ± 34.4	0.38 ± 0.16	0.27 ± 0.07	0.08 ± 0.02	0.07 ± 0.02
(Range)	(7.53–45.4)	(12.3–45.9)	(0.85–3.18)	(0–120)	(0.15–0.61)	(0.09–0.38)	(0.05–0.13)	(<0.01–0.07)

both with/without PEG, included only leaf abundance, though their ΔAICc values (2.51) were higher than the cut-off of 2.0. This result indicates that these traits were not strongly associated with leaf selection in guerezas.

By contrast, linear models for the percentage of time spent eating young leaves indicated a positive effect of digestibility (both with and without PEG; **Table 4** and **Figures 2a,b**). Additionally, other models with ΔAICc values of <2.0 included CP, TA, CL, toughness, and indicators of secondary compounds (**Figures 2c–g**). The animals spent more time eating less tough leaves with more CP, but the trend for the other nutrients was unexpected as the animals spent more time eating leaves containing less CL and TA and more secondary compounds.

DISCUSSION

Leaf Toughness and Digestibility

The toughness of young leaves was negatively correlated with CP and fiber (NDF), which are important nutritional factors that influence leaf selection in colobine monkeys (e.g., Fashing, 2001; Chapman and Chapman, 2002; Evans et al., 2021). Thus, the present study indicates that in leaf-eating primates, leaf toughness, as assessed by the oral sensation derived from mechanical properties (Dominy et al., 2001; Huang et al., 2010; Lucas et al., 2011), may be a proximate cue for these key nutrients, especially CP. However, the unexpected negative relationship with NDF indicates that NDF content alone may not be used as an indicator of toughness, as leaf toughness increases with increasing total bulk density and cellulose fraction but decreases with increasing hemicellulose and lignin content (Kitajima et al., 2016). Similarly, a negative correlation between NDF content and toughness has been detected in leaves from the island of Borneo (Matsuda et al., 2017). Thus, not only NDF but also ADF and lignin content should be simultaneously evaluated in relation to leaf toughness to further understand the effects of fiber.

In addition to CP and NDF contents, we also found that leaf toughness was negatively correlated with indicators of secondary compounds, although both toughness and chemical toxicity are expected to increase with leaf age (McKey, 1974; Rhoades and Cates, 1976; Lowman and Box, 1983). Nonetheless, a meta-analysis of 50 studies examined plant growth, plant defense and herbivory in relation to resource availability across latitude and ontogeny, showing that secondary compounds such as phenols and tannins do not exhibit generalizable associations with several leaf traits, including toughness (Endara and Coley, 2011); this may be because the properties and functions of these secondary compounds vary greatly across individual plant species (Kitajima et al., 2012).

The positive relationship between leaf toughness and TA content has, to our knowledge, not been previously reported; whether this is a general trend or specific to our study area would need to be clarified in future studies. Finally, as indicated in some primates (Lucas et al., 1998; Dominy and Lucas, 2001), visual selection of chemical and/or mechanical properties may be an important factor for leaf selectivity in colobines; the color of leaves often changes from red/yellow-green to dark green depending on their age. Future research should consider the associations between the above factors in addition to leaf color and their toughness.

As predicted based on previous studies using both enzymatic and rumen fluid *in vitro* digestibility assays (Choo et al., 1981), there was a negative relationship of digestibility with some chemical properties in leaves, particularly fiber and condensed tannins. As dietary choice in folivorous primates is generally thought to be influenced by nutritional requirements, dietary constraints on fiber intake and the avoidance of undesirable secondary compounds (Freeland and Janzen, 1974), our findings support the adaptive significance of such dietary choice.

Selection Between Eaten and Not Eaten Leaves

At a broad level, we found that none of the evaluated factors, including the chemical and mechanical properties, digestibility, toughness and abundance of leaves, affected whether guerezas consumed leaves or not. As discussed for Kibale (Evans et al., 2021), which is geographically close to our study site, the overall high level of protein and low level of fiber in the young leaves at our site (**Table 3**) may have contributed to this result. Indeed, the non-consumed young leaves in our study site had higher CP and lower NDF contents than the young leaves eaten by other foregut-fermenting colobines (e.g., *Presbytis rubicunda* and *Nasalis larvatus*) living on the island of Borneo (Matsuda et al., 2013). Thus, the present results support the hypothesis that leaves containing proteins are actively selected only when protein is limited in the environment (Oftedal, 1991; Ganzhorn et al., 2017; Evans et al., 2021). It is important to note, however, that the study group relied on young *C. durandii* leaves, upon which they fed heavily throughout the study period (58%) (Matsuda et al., 2020). In line with observations of the quality of these leaves in Kibale, Uganda (Chapman et al., 2003; Harris and Chapman, 2007), we found that the leaves were nutrient dense (the second-highest CP content) with a high digestibility, possibly reflecting low contents of difficult-to-digest fiber and secondary compounds, and were relatively abundant (i.e., easy to find and access; Matsuda et al., 2020). Altogether, this indicates that these factors played a role in the high occurrence of these leaves in the diet of the guerezas observed in the present study. Thus, these factors would potentially have an effect on dietary selection.

Selection Within the Eaten Leaves

We found that CP content, digestibility and toughness played an important role in influencing the dietary choices of guerezas, based on a fine grade analysis that considered dietary choice in relation to the percentage of foraging effort devoted to specific items amongst those selected. As mentioned above, the amount of protein in the leaves from this study site was generally high; thus, in terms of selectivity among the eaten leaves, we expected that the guerezas would select leaves on the basis of fiber rather than protein content (e.g., McKey et al., 1981; Chapman et al., 2004; Fashing et al., 2007). As such, the selection of leaves with more protein is difficult to explain. Instead of CP, the available protein (i.e., CP minus the fiber-bound protein), which is suggested to be a more relevant measure (Evans et al., 2021), could theoretically explain our results; however, since available protein and CP are generally positively correlated (Rothman et al., 2008), the use of CP appears nevertheless justified. It is possible that factors other than protein level itself drove dietary selection.

Conversely, our results outlining the selection of more digestible and less tough leaves is in agreement, albeit indirectly, with those of previous studies, which revealed a preference for leaves with lower fiber contents. Leaf NDF content was found to be negatively related with digestibility (**Table 2**); therefore,

TABLE 4 | Summary of model selection for linear models used to examine the effect of consumed young leaf chemical properties, abundance, digestibility with PEG (A) and without PEG (B) and toughness on the percentage of feeding time (only models with ≤ΔAIC 2 are shown).

(A)	Intercept	Abundance	Crude protein	Total ash	Crude lipid	NDF	Digestibility with PEG	Toughness	Indicator of secondary compounds	df	Log-likelihood	AICc	Δ AIC	AICc weight
	−7.63				−0.34		0.12			4	−34.4	79.6	0	0.10
	−7.10						0.14	−1.17		4	−34.5	79.8	0.21	0.09
	−8.06						0.11			3	−36.1	79.9	0.29	0.09
	−6.78				−0.32		0.15	−1.07		5	−32.7	80.0	0.39	0.09
	−8.35						0.18	−1.55	0.20	5	−33.0	80.5	0.94	0.05
	−12.5		0.21	−0.39			0.15		0.30	6	−31.0	81.0	0.94	0.05
	−5.55			−0.22			0.16	−1.34		5	−33.3	81.2	1.42	0.04

(B)	Intercept	Abundance	Crude protein	Total ash	Crude lipid	NDF	Digestibility without PEG	Toughness	Indicator of secondary compounds	df	Log-likelihood	AICc	ΔAICc	AICc weight
	−8.35						0.18		0.39	5	−33.0	80.5	0	0.08
	−12.5		0.21	−0.39			0.15		0.45	6	−31.0	81.0	0.48	0.06
	−6.44				−0.37		0.10			4	−35.1	81.1	0.56	0.06
	−6.89						0.10			3	−36.9	81.5	0.96	0.05
	−7.80				−0.26		0.18		0.34	6	−31.7	82.4	1.91	0.03
	−8.85						0.13		0.23	4	−35.7	82.5	1.93	0.03

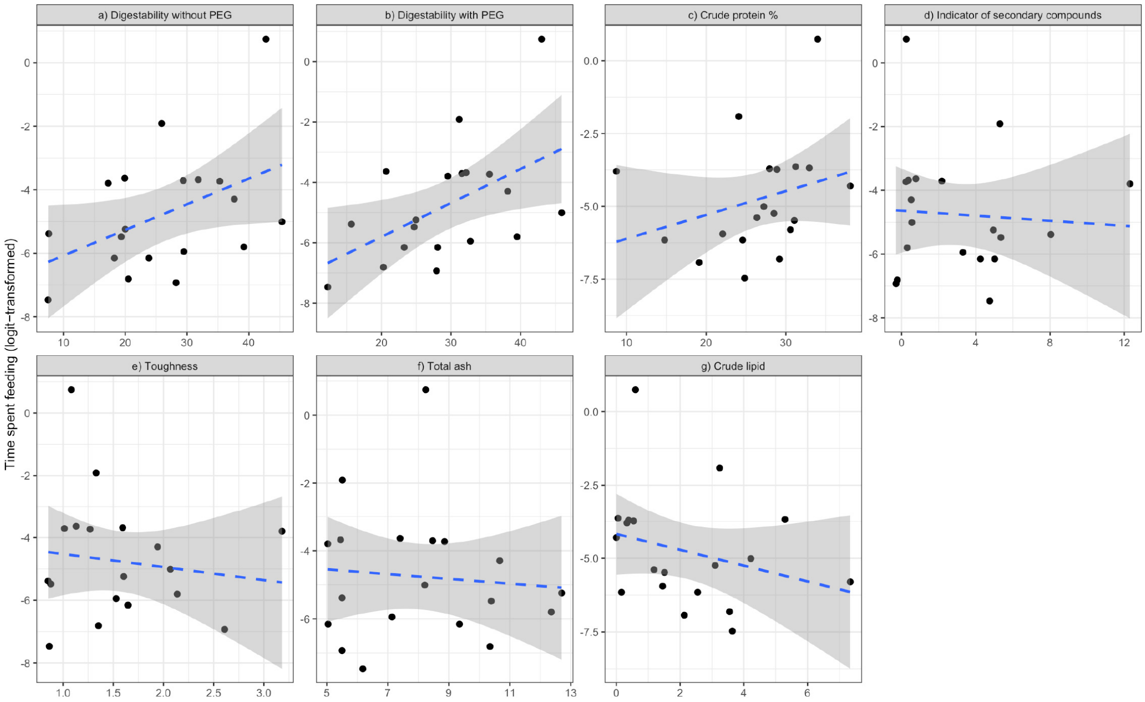

FIGURE 2 | Relationships of the proportion of time spent feeding (logit transformed) with *in vitro* digestibility **(a,b)**, chemical properties **(c,d,f,g)** and toughness **(e)** of consumed leaves by study guerezas, based on the model selection **Table 4**. Blue dotted lines and shaded areas represent the linear regressions estimated by the "lm" method in R for the observed samples and their 95% confidence interval ranges, respectively.

digestibility, which can quantify leaf quality as represented not only by fiber but also secondary compounds, may be the main factor that explains the guerezas' dietary choices in this study. The unexpected negative relationship between NDF and toughness may have led to the selection of tender, but NDF-rich, leaves in our study. Leaf toughness has a decisive influence on colobine feeding behavior in terms of nutrients such as fiber as well as foraging/ingestion efficiency. In fact, ingestion rate (g/min) in Angolan black-and-white colobus monkeys (*Colobus angolensis palliatus*) is negatively correlated with leaf toughness, whereas masticatory investment (chews/g) is positively correlated with leaf toughness (Dunham and Lambert, 2016). Thus, choosing tender leaves is a reasonable strategy to increase the consumption of better quality foods that are high in protein (but NDF-rich) and can be ingested efficiently.

Outlook

Broadly speaking, we showed that leaf CP content and digestibility in relation to NDF content, secondary compounds and toughness were associated with the dietary choices of guerezas in our study site. Generally, this result is consistent with the food selectivity trends of guerezas documented at other study sites where multiple groups have been surveyed (Chapman et al., 2004; Fashing et al., 2007). However, because we only assessed a single family group, we cannot claim that the whole guereza population at Kalinzu shows the same behavior. Additionally, the potential bias of our study results may be created by the mismatch in time between behavioral data and leaf analyses as leaf traits may vary depending on the seasons (Chapman et al., 2003). Nonetheless, since temporal fluctuations of nutrients in tropical plant material, are smaller than inter-individual variations within the plant species in Kibale National Park, Uganda, it is recommended to sample from several trees at a point in time, as we performed in this study, rather than sampling over time (Chapman et al., 2003). However, the most accurate assessment of nutritional intake can be obtained by analyzing plant materials collected from specific trees selected for consumption, and this should be a future challenge in exploring the more detailed dietary choices of the study animals.

The results of this study reveal some similarity to the food selection practices of *N. larvatus*, an Asian colobine that is fairly comparable (Matsuda et al., 2017); however, leaf selectivity within the preferred plant species differed, since *N. larvatus* are more dependent on the abundance of the plant species rather than on its chemical and mechanical properties as well as digestibility. As in this study and that conducted by Matsuda et al. (2017), examining the dietary choice mechanisms of colobines from a variety of indices contributes to establishing relevant proxies and also allows for an understanding of the various functional properties of plants that are specific to each region. Further investigation of these plant properties in different geographical regions may aid in understanding the diverse interspecific and intraspecific foraging strategies of colobines, which may have arisen as an adaptation to the various functional properties of plants.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the study was based on the observation, but all research was conducted in compliance with animal care regulations and applicable Uganda laws.

AUTHOR CONTRIBUTIONS

IM, MC, and JH conceptualized the initial idea and drafted the manuscript. IM performed the behavioral observation and sample collections with measurement of toughness in the field, arranged the chemical analysis of plant samples, and performed and interpreted the statistical analyses. JH conducted the digestibility analysis. CH, HI, TY, and DB arranged the sampling in the field. All authors contributed to the final version of the manuscript.

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REVIEW
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What Are the "Costs and Benefits" of Meat-Eating in Human Evolution? The Challenging Contribution of Behavioral Ecology to Archeology

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Despite the omnivorous diet of most human populations, meat foraging gradually increased during the Paleolithic, in parallel with the development of hunting capacities. There is evidence of regular meat consumption by extinct hominins from 2 Ma onward, with the first occurrence prior to 3 Ma in Eastern Africa. The number of sites with cut-marked animal remains and stone tools increased after 2 Ma. In addition, toolkits became increasingly complex, and various, facilitating carcass defleshing and marrow recovery, the removal of quarters of meat to avoid carnivore competition, and allowing the emergence of cooperative (i.e., social) hunting of large herbivores. How can we assess the energy costs and benefits of meat and fat acquisition and consumption for hunter-gatherers in the past, and is it possible to accurately evaluate them? Answering this question would provide a better understanding of extinct hominin land use, food resource management, foraging strategies, and cognitive abilities related to meat and fat acquisition, processing, and consumption. According to the Optimal Foraging Theory (OFT), resources may be chosen primarily on the basis of their efficiency rank in term of calories. But, could other factors, and not only calorific return, prevail in the choice of prey, such as the acquisition of non-food products, like pelts, bone tools or ornaments, or symbolic or traditional uses? Our main goal here is to question the direct application of behavioral ecology data to archeology. For this purpose, we focus on the issue of animal meat and fat consumption in human evolution. We propose a short review of available data from energetics and ethnographic records, and provide examples of several various-sized extant animals, such as elephants, reindeer, or lagomorphs, which were some of the most common preys of Paleolithic hominins.

Keywords: Pleistocene, energetics, extinct hominins, behavioral ecology, meat and fat consumption

INTRODUCTION

Energetics (e.g., food accessibility and availability, energy intake and balance. . .) comprise critical information for enhancing our understanding of human evolution (Aiello and Wheeler, 1995; Leonard and Robertson, 1997; Aiello and Wells, 2002; Snodgrass et al., 2009; Isler and Van Schaik, 2014; Burini and Leonard, 2018). A shift to a more energetical-rich food, such as meat, contributes to meeting elevated daily energy requirements (Pontzer, 2017; Pontzer and Wood, 2021). Meat consumption behavior and hunting are also observed in non-human primates. For example, bonobos focus primarily on small herbivores. Chimpanzees occasionally hunt monkeys using tools (Pruetz et al., 2015), but process carcasses without any use of tools. Meat represents less than 0.01–0.19 kg/day in their diet and only small proportions of their feeding time (Watts, 2020). During human evolution, meat consumption seems to increase and to become less sporadic than in extant non-human primates. As a famous primatologist, Washburn, expressed: "The taste for meat is one of the main characteristics distinguishing man from the apes, and this habit changes the whole way of life. It is therefore important to date the beginning of hunting in order to interpret the origin of human behavior" (Washburn, in Brain, 1981).

The purpose of this short literature review is to present the main steps of meat-eating in human evolution, and to discuss its cost and benefits in terms of biological and sociological aspects. In order to do so, we present different approaches for addressing the energetics of past hominins, crossing extant and archeological data. Finally, we discuss the relevance of paleoanthropological and archeological data in the context of meat consumption and assess the interests and limitations of applying behavioral ecology to archeology.

MEAT-EATING IN HUMAN EVOLUTION: ARCHEOLOGICAL EVIDENCE

The first occurrences of meat consumption by early hominins are recorded in Africa around 3.4 Ma at Dikika, Ethiopia (McPherron et al., 2010; Thompson et al., 2015), although the identification of the butchery marks is still questioned (Domínguez-Rodrigo et al., 2010, 2011; McPherron et al., 2011). Pliocene stone tools discovered at Lomekwi 3, Kenya, 3.3 Ma, support the hypothesis of stone tool making by Pliocene hominins more than 3 Ma ago, 500,000 years before the emergence of the *Homo* genus (Harmand et al., 2015). In addition, dental and cranial morphology, gut size or endurance running point to increased meat and fat consumption among Late Pliocene and Early Pleistocene African hominins (Aiello and Wheeler, 1995; Teaford and Ungar, 2000; Teaford et al., 2002; Bramble and Lieberman, 2004; Ungar, 2004; Daegling and Grine, 2007; Ben-Dor et al., 2021), as do stable isotopes analyses (Balter et al., 2012; Martin et al., 2020). We observe an increased number of sites with cut-marked animal remains and stone tools after 2 Ma, in eastern Africa (Bunn, 1981; Potts and Shipman, 1981; De Heinzelin et al., 1999). For example, the Oldowan site of Kanjera (2 Ma), South Kenya, yielded numerous bone elements processed by hominins, comprising small as well as medium-sized bovids, highlighting meat consumption and also the first evidence of hunting small animals (Ferraro et al., 2013). In parallel to this early consumption of small animal tissues, some evidence shows the input of aquatic and plant-based resources. Meat from terrestrial mammals was not the only, nor the main source of protein. For example, in the Koobi Fora Formation, Kenya, some crocodile, fish and turtle remains bearing cut marks highlight the exploitation of water habitats by early *Homo erectus* (i.e., *H. ergaster*) (Braun et al., 2010; Archer et al., 2014). Besides, dental wear patterns and isotope ratios indicate wide diversity in the diet of Late Pliocene and Early Pleistocene hominins, including plants and hard foods such as nuts, seeds and underground storage organs (Ungar and Sponheimer, 2011; Balter et al., 2012; Grine et al., 2012). Animal fats were also an important source of calories for past hunter-gatherers, and large herbivores in particular provide omega-3 fatty acids (Guil-Guerrero et al., 2014, 2015).

Toolkits may also have been essential to hominins for butchering carcasses, with cutting edges for processing soft tissue as well as percussion tools to extract marrow. With the onset of the Acheulean and the emergence of *H. erectus* sensu lato populations in Africa, between 1.9 and 1.7 Ma (Lepre et al., 2011; Hammond et al., 2021), we observe a dietary change with greater evidence of carnivorous and predatory behavior in faunal assemblages (Shipman and Walker, 1989; Echassoux, 2012; Pante, 2013; Domínguez-Rodrigo et al., 2014; Diez-Martín et al., 2015; Arriaza et al., 2017; Yravedra et al., 2020). However, although meat consumption occurred quite early in human evolution, common meat consumption, complex forms of cooperative hunting, entire butchery sequences and stone and carcass transport, which require advanced cognitive skills such as planning and more decision-making, seem to have developed later, after 1 Ma, throughout the African continent and the Levant in conjunction with early Middle Pleistocene environmental changes (Clark et al., 2006; Rabinovich et al., 2008; Forrest et al., 2018; Altamura et al., 2019; Daujeard et al., 2020).

Later, in Western Europe, the large quantities of herbivore remains found in Middle Paleolithic sites (c. 400–40 ka) (Gaudzinski and Roebroeks, 2000; Costamagno et al., 2006; Daujeard et al., 2012; Niven et al., 2012; Rendu et al., 2012), stable isotope ratios (Bocherens et al., 2005; Wißing et al., 2016; Jaouen et al., 2019) and tooth wear data (Estalrrich et al., 2017), highlight the high intake of animal proteins in the Neanderthal diet. Neanderthals could rely for up to 80% on animal protein and 20% on plant proteins (Naito et al., 2016), making them the most emblematic carnivorous and competitive big game hunters among extinct hominins (Karavanić et al., 2000). Despite this mostly carnivorous diet, more recently, dental calculus residues show that many Neanderthal groups consumed plants for food, medicinal or gustatory purposes (mushrooms, pine nuts, leguminous plants, etc.) over a widespread area ranging from the Mediterranean Basin to Central Europe (Henry et al., 2011; Hardy et al., 2012; Krief et al., 2015; Weyrich et al., 2017; Power et al., 2018). Moreover, in their recent article, Hardy et al. (2022) emphasize the importance of plants in nutrition for all hominin species, including Neanderthals, through indirect evidence, such as physiological requirements.

For Pleistocene Anatomically Modern Humans (AMH), interpretations also point toward a high quantity of meat in their diet, predominantly from large game (Prat et al., 2011; Drucker et al., 2017; Ben-Dor et al., 2021). Although small game was consumed since the Early Paleolithic (Fernández-Jalvo et al., 1999; Braun et al., 2010) and the Middle Paleolithic (Hardy and Moncel, 2011; Cochard et al., 2012; Hardy et al., 2013; Blasco et al., 2016; Morin et al., 2019; Pelletier et al., 2019; Guillaud et al., 2021), we note an increase in small prey and fish at the end of the Upper Paleolithic in Europe and the Levant (Stiner et al., 2000; Costamagno and Laroulandie, 2004; Rufà et al., 2018). Concerning carbohydrates intake in the AMH diet, alongside the more numerous direct evidence, recent studies on the oral microbiome highlighted a high degree of similarity between modern humans and Neanderthals, with the specific acquisition of starch digestion (Fellows Yates et al., 2021).

Finally, whether prey species were passively or actively scavenged, trapped or hunted, the intensification of animal meat and fat in the diet of extinct hominins exposes them to competition with various other predators and scavengers, increasing interactions: direct attacks, passive confrontations, dispersals, commensalism, etc., and mutual contributions: providers of carrion, models for hunting strategies, etc. (Marean, 1989; Shipman and Walker, 1989; Turner, 1992; Rodríguez et al., 2012). Whatever the types of strategies used and the amount consumed, the consumption of meat and fat may have had significant consequences on human evolution in terms of biology, societies and also in terms of energetic costs and benefits.

CONTRIBUTION OF ECOLOGICAL MODELS AND EXTANT DATA TO THE STUDY OF PAST HOMININ DIETS

Ecological Models

In order to address subsistence practices and the energetics of past hominins, a multi-proxy approach is necessary, taking into account various factors: hominin capacities (biological, social and cultural features), paleoenvironmental constraints (biomass, prey availability, seasons, topography, other competitors, etc.), archeological and geochemical data (faunal remains, isotopes, etc.) and actualistic data and ecological models, used for example in human behavioral ecology (HBE) (Smith, 1992). HBE is a neo-Darwinian approach in which changes in behavior may result from natural selection (adaptation to the environment), rather than from cultural motivations. HBE emerged in the mid-1970s with the application of optimal foraging models to hunter-gatherer decisions relating to resource selection and land use (Winterhalder and Smith, 2000; Codding and Bird, 2015).

In the 1980s, a theory developed by ecologists, called The Optimal Foraging Theory (OFT) (Stephens and Krebs, 1986; Pyke and Stephens, 2019), was applied to anthropology and archeology to specifically explain dietary patterns in hunter-gatherer societies (Smith, 1979; Winterhalder, 1981; Smith et al., 1983). OFT provides predictions and valuable models for grasping the relations between the environment and foragers in the past. What should be eaten? Where should food be sought and how large a group is needed to catch and exploit the food? According to the OFT, resources may be chosen primarily on the basis of their efficiency rank in term of calories. The most current of these foraging models is diet breadth, also called prey-choice model (PCM) or optimal diet (Winterhalder and Smith, 2000; Bird and O'Connell, 2006). According to this model, high-ranked resources are pursued whenever encountered, and lower-ranked resources are included in the diet depending on encounter rates with higher ranked resources. Thus, prey choice takes into account various parameters such as the main goal, which corresponds to the maximization of foraging efficiency, currency, which is usually a measure of energy costs and benefits; constraints, which are all the limiting factors, such as the time spent foraging, processing or digesting capacities; and the alternative options for making a decision, which incorporate the possible set of food resources, daily needs and other ways of spending time (childcare for example).

According to these models, energy is one of the main parameters influencing subsistence strategies in past hunter-gatherer societies, it is important to calculate the return rate of the animal. The Energy Cost-benefit or Post-Encounter Return Rate (PERR) or Efficiency rank is defined as the ratio of the Energetic benefit of the animal (expressed in kcal) to the Energetic cost related to searching and handling time (expressed in person-hours). Handling time corresponds to the time spent pursuing and dispatching prey, carcass processing and transport and consumption (chewing and digesting time). The latter depend on several parameters, such as the type of prey (size, weight, age, aggressiveness, encounter rate, etc.), consumed body parts, season, topography, distance, group size, other competitors, etc.

Extant Data on Animal Nutrients and Human Biology

The energy intake and nutrients supplied by terrestrial animals correspond to meat, fat, yellow, and red marrow, brain, tongue, viscera, etc. Meat and marrow nutrients provide proteins (amino acids), fats (saturated and unsaturated fat), vitamins (A, B1, B2, B3, B6, B12, and C) and minerals (Iron, Calcium, Zinc). Fat is the most energy-dense macronutrient (Ben-Dor et al., 2021). For example, lean beef meat provides between 100 and 200 kcal/100 g, but beef fat contains about twice as many calories (900 kcal/100 g) as protein or carbohydrates (400 kcal/100 g). Indeed, although meat-eating is of high calorific value, it induces high energy expenditure for the elimination of nitrogenous waste products. As a result, a diet rich in lean meat requires very high daily food rations to cover body energy requirements. In addition, excessive protein consumption leads to liver and kidney disorders. Excessive animal protein intake may lead to protein toxicity which can be dangerous for pregnant women and new-borns (Fiorenza et al., 2015). These deficiencies and health risks can be overcome by increasing the fat intake in the diet. Fat has a high energy value, and enables gluconeogenesis, a metabolic process occurring primarily in the liver and kidneys that produces carbohydrates from protein and fat (Speth and Spielmann, 1983; Speth, 2010). These advantages therefore go a long way to explaining why Paleolithic human groups sought to harvest fat wherever it was available, including fat contained in the marrow and cancellous tissue of very large and large mammals long bones (Costamagno and Rigaud, 2013; Smith et al., 2015; Ben-Dor et al., 2016; Blasco et al., 2019a; Boschian et al., 2019; Morin, 2020; Dodat et al., 2021). The preparation of broths based on fat contained in bone tissue observed among the Nunamiut by Binford (1978) suggests that such processes may have existed in Paleolithic societies (Speth, 2015). Moreover, in order to avoid excessive meat protein, in addition to animal fat, other alternative food resources, such as plants, might have been incorporated in the diet (Henry et al., 2011, 2014; Fiorenza et al., 2015).

Since the 1970s, the plethora of ethnographic studies of hunter-gatherer societies have provided abundant data on human biology and diet, and fostered the development of ethnoarchaeological research through the 1980s and 1990s (Binford, 1978; Keene, 1985; O'Connell et al., 1988a, 1990; O'Connell and Marshall, 1989; Bartram, 1993; Bunn, 1993, 1994; Kelly, 1995; Bartram and Marean, 1999). We know for example that we have a daily energy expenditure of 2,000–3,000 kCal per day, which is related more to body size, age, and sex than to cultural differences (Pontzer et al., 2012). Relative to other great apes, hunter-gatherers spend more daily energy for food-finding, but with a greatest return rate, making possible the sharing with others, and thus the possibility for some to carry out tasks other than foraging (Kraft et al., 2021). The similarity in daily energy expenditure among hunter-gatherers and sedentary Westerners suggests that the effect of marked lifestyle differences is minor and that differences between populations result primarily in energy intake, rather than expenditure. In the same way, variation in the diet is mainly related to temperatures and primary production, for example, hunting territories are generally larger in northern latitudes (Kelly, 1995). Regarding the proportion of meat, animal fats or plants in the human diet, we have to be careful with the data from present-day hunter-gatherers. Environmental conditions, technical, and physiological adaptations must prevent us from making direct analogies with Pleistocene hominins, and even more so with the earliest ones (Ben-Dor and Barkai, 2020; Ben-Dor et al., 2021).

Eating Raw or Cooked Meat: What Is the Energetic Impact?

The control of fire and its use for cooking marks another critical shift in the diet. Indeed, despite the apparent importance of meat in human evolution, some studies (Carmody and Wrangham, 2009) showed that a raw food diet provides insufficient energy for the maintenance of body weight, suggesting that food processing and cooking are very important. Indeed, when starch or proteins are cooked, they are more tender, more digest, mastication is facilitated (reduction of chewing time), the cost of digestion is reduced and energy extraction per unit mass increases (Wrangham et al., 1999; Carmody and Wrangham, 2009; Carmody et al., 2011; Hardy et al., 2015). Furthermore, cooking kills food pathogens. However, iron and certain vitamins, such as for example vitamins B12 and C (which primates are unable to synthesize), decrease with high temperatures and cooking time. Cooking can be quite costly in terms of energetic expenditure in terms of fuel collection, the time needed to make and maintain fire, and requires some cognitive skills, such as for example for fuel collection (choice of wood, bones, stones etc.), and fireplace location (Henry et al., 2018; Magargal, 2022). Cooking or fire use was initially very occasional, and could have occurred with *H. erectus* in Africa c. 1.8 Ma ago. This hypothesis is based on indirect evidence of hot springs (Sistiaga et al., 2020), thermally altered lithics and bone fragments at 1.5 Ma in Kenya (Hlubik et al., 2017), microstratigraphic evidence at 1 Ma in South Africa (Berna et al., 2012), and the decrease in the size of the digestive system (see below "Expensive Tissue Hypothesis"). Therefore, this indirect evidence predates the first evidence of the control of fire in the Near East at 790 ka (Alperson et al., 2004; Alperson-Afil, 2008) and the oldest evidence of the habitual use of fire attested around 300–400 ka in Europe, Africa and the Levant, which suggests that this behavior is relatively recent (Roebroeks and Villa, 2011; Shahack-Gross et al., 2014; Barkai et al., 2017; Richter et al., 2017; MacDonald et al., 2021).

Aiello and Wheeler (1995) put forward the "Expensive Tissue Hypothesis" to explain how primates can have relatively large brains without a high basal metabolic rate. For those authors, the increased energetic demands of a larger brain are compensated by the reduction in the mass-specific metabolic rates of other tissues, such as the gastro-intestinal tract. Their analyses in human and non-human primates infer coevolution between brain and gut sizes, which is dependent on energy intake and could be determined by dietary quality. They consider that hominins, especially after 2 Ma (e.g., early *H. erectus* sensu lato), had small guts, and would have required the use of fire and cooking to efficiently process difficult-to digest food, such as meat. However, some authors consider that this trade-off scenario seems to be insufficient (Navarrete et al., 2011; Isler and van Schaik, 2012), and they stress that brain size is not correlated with other energetic expensive organs or with digestive tract mass, and that encephalization and fat storage in primates are strategies to buffer against caloric shortfalls. Furthermore, Cornélio et al. (2016), revisiting correlations between brain size and cooking, showed that large primate encephalization occurred long before the control of fire and that hominins were likely to obtain enough calories from raw meat to afford brain size increase. Indeed, processing methods such as pounding (Zink et al., 2014; Zink and Lieberman, 2016), or eating rotten or putrefied meat, also result in an important increase in energy compared to unprocessed raw diets (meat or tubers). In addition, such methods preserve vitamins, favor pre-digestion and do not require fuel (Speth, 2017). Likewise, other studies propose that the increased need for more energetical-rich nutrients due to reduced gut size might also have been compensated by animal fat (Ben-Dor et al., 2011), or even by semi-digested chyme, i.e., gastrophagy (Buck et al., 2016).

Meat-Eating and the Origin of Social Cooperation and Food Sharing

Meat involves a relatively high level of cooperation. Compared to plants, meat is difficult to obtain, and very demanding in both time and energy. This becomes particularly critical when the subsistence strategy focuses on big game, where cooperation is often needed to acquire resources and fend off predators. In such cases, distribution needs to be efficient within the group and all the participants have to receive a payoff (Alvard, 2011). Food sharing, and in particular meat sharing, is thought to be central to the evolution of hominin behavior and to hunter-gatherer economics where food transfer practices vary greatly, depending on resource availability in the environment, or/and social organization (Hawkes et al., 1991; Winterhalder, 1997; Lee and Daly, 1999; Enloe, 2003). Food sharing reduces the risk of caloric shortfall, especially when it concerns large animals, which are high-risk food as they are difficult to obtain but also high-reward food. Hunting is considered to be one of the most difficult foraging activities. Direct encounters with big game and successful capture require substantial skills and knowledge sharing which develop at least 10 years after attaining adult body size (Gurven et al., 2006). In most hunter-gatherer populations, the meat of big animals is widely shared with the opportunity to get it back later. The cost of sharing with the whole group is quite low, as the total amount of meat cannot be eaten at one time by the hunter's family. On the contrary, the benefits of the reciprocity are quite high, as sharing avoids meat spoilage, long-term food storage and reduces the risk of nutrients shortfalls, especially for large prey such as elephants (Hawkes et al., 1991; Enloe, 2003; Gurven and Jaeggi, 2015; Barkai, 2019). Hadza populations consider carcasses of large sized animals as public goods. There are few nutritional advantages to being an efficient hunter, and the benefits to the generous sharers might only be their hunter reputation (Kaplan et al., 1985; Stibbard-Hawkes et al., 2020).

Hominins could have used different acquisition modes over time to obtain meat from small or large animals: trapping, passive or confrontational scavenging, ambush or pursuit hunting using short or long distance weapons, hand capture of small-sized prey, etc., which favored the development of social cooperation and food sharing (Domínguez-Rodrigo, 2002; Stiner et al., 2009; Gaudzinski-Windheuser et al., 2018; Conard et al., 2020). Primary distribution occurred at the kill site, as the carcass was partitioned for transport. Secondary distribution, which is redistribution to family, took place at the campsite or the consumption area. These two stages can be observed in the archeological record thanks to the spatial distribution and butchering patterns of the carcasses. However, the origins of food sharing and its definition and purpose are still debated in evolutionary anthropology and Paleolithic archeology (Isaac, 1978; Kaplan et al., 1985; Blurton Jones, 1987; Hawkes, 1991; Winterhalder, 1996, 2001). It is reasonable to expect that Pleistocene hominins lived in social groups, but food-sharing patterns must have differed a lot through time and depended on the size of game (Stiner et al., 2009). Willems and Van Schaik (Willems and van Schaik, 2017) suggest that at the time of the emergence of the *Homo* genus, the social organization of *H. ergaster* revolved around reduced fission-fusion dynamics and very large multi-male groups, which could have helped to defend the group against predators. Through time, when hominins moved toward higher latitudes (further north), increasingly complex multilevel fission-fusion social systems could have helped hominins to adjust foraging patterns, constrained by large group size, low population densities and increased foraging demands (Grove et al., 2012). Furthermore, the most common anthropological scenario also suggests a link between the transition toward eating a high-quality diet, such as meat, for example, and cooperation among hominins (including care of the young, protection from predators, group hunting, and food storage) (O'Connell et al., 1988b, 2002; Hawkes et al., 2001; Bramble and Lieberman, 2004; Pontzer, 2012). Intergenerational cooperation brings increased energetic benefits, with the coevolution of increases in the duration of lactation, gestation, longevity, neonate and adult body mass and daily energy expenditure, but a decrease in sexual dimorphism (Smith et al., 2012). Indeed, according to Smith et al. (2012) evidence from carnivores indicates that both the pace of reproduction and the emergence of cooperative defense against predators can respond in a flexible fashion to variations in the availability and acquisition of energy-rich foods. Thus, for those authors, it is possible that similar flexibility influenced shifts in reproductive investment and reproduction rates among hominins.

Another adaptive reason why Late Pliocene and Early Pleistocene hominins had to amplify forms of cooperation regarding immature individuals is related to human life history, with juveniles remaining dependent for a longer time on mothers than other species. In the course of human evolution, this was made possible through the support of group members other than the mother, i.e., "food transfer between alloparents and offspring: cooperative breeders" (e.g., Burkart et al., 2009; Hrdy, 2009; Strassmann and Kurapati, 2010; Kramer et al., 2015). Cooperative breeding, which affects parental care (shorter birth intervals, juvenile dependence), is presumed to appear in the Lower Pleistocene with early *H. erectus* (O'Connell et al., 1999; Hrdy, 2009; van Schaik and Burkart, 2010). Indeed, Aiello and Key (2002), suggest that *H. erectus* females were able to cope with increased energetic costs per offspring (daily energy requirements during gestation and lactation) by shortening interbirth intervals and cooperating with others in feeding dependent children. Moreover, Wrangham and Conklin-Brittain (2003) have also suggested that cooking, which makes raw food soft enough for young individuals to chew, may have facilitated shorter inter-birth intervals.

To conclude, animal acquisition and consumption represent an undeniable advantage in terms of time and energy benefits, by providing considerable quantities of proteins, fat and other nutrients. However, it may also sometimes constitute a high-cost food source, and if considering only meat, it can be even unhealthy in excessive amounts. Hunter-gatherers should not exceed a maximum quantity of protein intake (plant and animal) per day, and so they must also obtain a large part of non-protein food in their environment (fat and carbohydrates) (Speth, 1989). As a matter of fact, big-game hunting is not always advantageous for feeding a human group. The risk of failing, the time to pursuit, the type and size of the prey, their physiological condition throughout the year, sometimes with a scarcity of fat, and many other parameters, all challenge the prominence of hunting large mammals in the early human diet (Speth, 2010).

THE CASE OF THREE TYPES OF PREY SIZE: AT THE CROSSROADS BETWEEN EXTANT AND ARCHEOLOGICAL DATA

We can hypothesize on the prey acquisition and carcass transport strategies developed by past hunter-gatherer societies using extant and energetic data. These strategies depend on several parameters in terms of energy costs and benefits: (1) the number of hunters; (2) the type of prey (size, weight, age, aggressiveness, encounter rate, etc.); (3) the nutritive value of chosen carcass elements; (4) the season; (5) the topography and the distance from the kill site to the camp; (6) the distribution within the group and repayment; and (7) the presence of other competitors; etc. Concerning the latter parameter, early experimental and actualistic research in African national parks yield a better idea of carcass availability in the environment, the degree of competition and resource partitioning strategies for the different predators and scavengers (Brain, 1981; Blumenschine, 1986; Brantingham, 1998; Domínguez-Rodrigo, 1999). Besides, as far as the weight of the animal is concerned, we know that for the Hadza in Tanzania, 80% of the anatomical elements of skeleton are abandoned at the kill site for large or very large adult animals, compared to only 30% for those of medium size, in relation with the cost/benefit rate of each carcass portion (O'Connell et al., 1990; Lupo, 2001). The age of the animal and season of death may also be relevant in the transport strategies. Adult marrow is richer than that of juveniles, and in the same way, marrow represents the last fat resource during the winter, which explains the interest for bones such as metapodials, which are poor in meat but rich in yellow marrow (Speth and Spielmann, 1983; Speth, 1987). Here, we will take the example of three animals of different sizes (elephants, reindeer, and lagomorphs) exploited by past and extant hunter-gatherers, and examine their specificities in term of energy and capture difficulty.

An adult elephant provides a huge amount of meat; almost two tons. Despite its weight, this colossal animal is not always sought by past and present hunter-gatherers. According to Lupo and Schmitt, whose data come from ethnographic and historic sources (Lupo and Schmitt, 2016): "Applications of the Prey Choice Model to ethnographic populations show that prey size does not always predict profitability." First of all, hunting failure has to be considered, considering many variables, including the prey itself. According to the authors, the bigger the prey, the more likely hunters are to miss it. Larger-sized preys are less abundant in the landscape, and hunters spend more time tracking them. The success rate for elephants is only 20% for Bisa hunters in Zambia, which drastically reduces the PERR. Secondly, the time spent pursuing the animal can be up to 38 h for an elephant. Lupo and Schmitt highlight the strong and positive correlation between the size of the prey and pursuit time. Lastly, large game requires extensive processing and transport efforts involving many individuals, with 86 h of butchering time for an elephant.

In comparison, for the Paleolithic, the role of megafauna in the hominin diet is often questioned. The association of megafauna with archeological sites is sometimes problematic and the full range of possibilities should be discussed. One of the critical factors for many of the megafauna sites is that some may be the results of scavenging or bone collecting for fuel, tools and building materials (Gaudzinski et al., 2005; Domínguez-Rodrigo et al., 2014; Lupo and Schmitt, 2016). Besides, zooarchaeological evidence of megafauna exploitation in Early and Middle Paleolithic assemblages is scarce, which rather supports the opportunistic role of megafauna during these ancient periods (Demay et al., 2012, 2016a,b; Smith, 2015). Nevertheless, the role of proboscideans in human evolution should not be minimized. In this regard it is important to notice that butchery and fracturing marks are particularly difficult to observe on pachyderm bones, as it was previously pointed out (Crader, 1983; Haynes and Krasinski, 2021). In the same way, a large quantity of food from Proboscideans in the Paleolithic has been highlighted by high ratios of nitrogen in humans (Wißing et al., 2016; Drucker et al., 2017). Yet, these data should be treated with caution as other parameters can induce high nitrogen levels, such as a diet based on aquatic resources, breastfeeding, putrefied meat or episodes of caloric shortfalls (Speth, 2017). Although evidence for elephant hunting is mostly provided for the Upper Paleolithic times (Svoboda et al., 2005; Agam and Barkai, 2018; Demay et al., 2021), for earlier periods there is the case of the Pleistocene elephant single-carcass sites, such as the Acheulean sites of Nadung'a 4, Kenya (Delagnes et al., 2006), or that of Barranc de la Boella, Spain (Mosquera et al., 2015). There are also the example of the Middle Pleistocene sites in the Latium in Italy with many Elephant remains (Anzidei et al., 2012; Boschian and Saccà, 2015). They have given rise to various hypotheses. Are they related to specific human behavior, to an exceptional preservation context or to a higher number of pachyderms in the environment?

Concerning reindeer, the two most famous ethnographic examples of reindeer husbandry and hunting in Northern latitudes are the Nunamiut (Alaska) and the Evenki (Russia), among others (Winterhalder, 1983; Costamagno and David, 2009). The Nunamiut are large bands of a hundred individuals. They are 80% dependent on reindeer hunts and can kill more than 200 reindeer for a year through the mass killing of migratory tundra gregarious reindeers (Binford, 1978, 1981). Evenki are small family groups of 5–10 individuals. Among the Evenki, Abe observed the kills of four woodland reindeer for 21 reindeer hunts for a year, which represents a very low success rate (19%) compared to those of the Nunamiut (43%) (Abe, 2005). Tracking a reindeer on foot can last more than 11 h, including kill site butchery. The PERR of a reindeer is thus 80,000 kcal/11 h, and lower once the success rate is considered.

To illustrate the exploitation of reindeer by past societies, we will take the example of a Middle Paleolithic site from south-eastern France. The Abri du Maras yielded Neanderthal occupations dated to around 50–40 ka for layer 4.1 (Moncel et al., 2021). Like many other archeological records with monospecific assemblages from the Middle Paleolithic of Western Europe, a great number of reindeers were present in the layer (88% of the NISP, representing 16 individuals), which also includes horse, bison, giant deer, red deer, ibex, and lagomorphs. Zooarchaeological analyses evidence a catastrophic age profile and autumnal kills, highlighting mass reindeer predation during migration events (Daujeard et al., 2019). At this camp site, we have *in situ* evidence of the reindeer exploitation of all the edible resources (marrow, meat, bone grease, etc.). The scarcity of the spongious part of the skeleton, axial parts (heads, vertebrae, and ribs), as well as girdles (pelvis and scapula), long bone epiphyses and short articular bones (carpals, tarsals, and phalanges), underlines either their abandon at the kill site and/or specific processing methods at the camp for grease bone extraction and/or for fuel. Only a few portions of the skeleton are represented in relation to their utility index (expressed in meat, grease, and marrow quantity). Anyway, although the choice of some portions is correlated to the Food Utility Index, bone grease as well as non-food products (like animal pelts) may also have mattered in the choice of past hunter-gatherers.

We have taken here the example of this faunal assemblage to illustrate Prey Choice Model and Carcass transport strategies. For that purpose, we assessed the energy intake from the faunal spectrum, and classified species according to their weight in meat. The total amount obtained is 3.5 tons of available meat if we count the whole carcasses of slaughtered animals, representing 4 M kcal, which can feed about 20 hunter-gatherers for two and a half months. In terms of Optimal Foraging Theory, some assumptions can be made:

- The selective diet would highlight a rich environment with a short encounter time;
- Reindeer probably had the highest encounter rate, with great autumnal migration events along the Rhone Valley;
- They were also safer and more easily transportable than Bison, while 16 reindeer are equal to two bison in term of meat weight;
- The few processed lagomorphs were probably the result of opportunistic encounters.

Finally, although this type of modeling opens up assumptions in terms of subsistence strategies, little can be said in the end as many occupations have certainly succeeded and mixed in this assemblage, as it was taken here as a whole.

Concerning lagomorphs, the encounter rate is much higher than for elephants (80% success) but they are much less productive. Indeed, the rabbit is small, only provides around 2.5 kg of meat and is in addition very poor in lipids, which can lead to protein toxicity called "rabbit starvation" (Cochard, 2004; Rufa Bonache, 2017). For lagomorphs, similarly, exploitation is scarce during the Early and Middle Paleolithic, with only a few archeological examples (Fernández-Jalvo et al., 1999; Blasco and Fernández Peris, 2012; Cochard et al., 2012; Hardy et al., 2013; Morin et al., 2019).

In spite of the low energy efficiency of lagomorphs when they are not slaughtered *en masse*, like other small preys, at the end of the Upper Paleolithic and during the Mesolithic, small prey hunting intensified. This could be explained by various hypotheses: cultural changes; environmental pressure with too many lagomorphs in a valuable territory; decrease of mobility and longer human occupations; or demographic pressure, which would have led to the broad-spectrum revolution. The demographic pulses of the UP and Epi-Paleolithic would have then forced the human diet to exploit fast-growing preys (Stiner et al., 2000).

DISCUSSION AND CONCLUSION: THE LIMITS OF APPLYING BEHAVIORAL ECOLOGY TO ARCHEOLOGY

Above, we saw how relevant energetic and ethnographic studies can be to human evolution. Here, we would like to address some of the more problematic points related to these approaches.

The Problem of the Scarcity of Archeological Evidence and Time Scales

To start with, it should be noted that data from extinct populations only yield isolated points in the paleoanthropological and archeological record. In addition, the range of error for the chronological framework could be around 50,000–100,000 years for Late Pliocene and Early Pleistocene periods, due to the dating methods used, and it is thus difficult to precisely link two different subsistence proxies. In addition, information on the diet consumed and the quality of the diet cannot be strictly compared between hominins and extant human and non-human primates. For hominins, dental microwear analyses provide data on the diet consumed a few days before the death of the individual. Isotopic analyses based on dental remains give some information of the diet consumed in early life. Furthermore, as data are cumulative, we only have an overall picture of the diet and it is impossible to gauge the diet consumed on a daily basis. Moreover, it is difficult to discern the ratio of meat in the diet of past hominins, and especially for the Late Pliocene and Early Pleistocene periods, although some new isotopic analyses using barium, calcium or zinc isotopes seem quite relevant for this purpose (Balter et al., 2012; Jaouen et al., 2016; Martin et al., 2020; Dodat et al., 2021).

Most of the time, Paleolithic sites are composed of palimpsests of multiple human occupations, often mixed with natural and carnivore deposits. Such mixed accumulations really challenge the reconstruction of ecological models, based on the balance between hominins' daily energetic needs, and the energetic intake provided by animals accumulated over very long time periods. Moreover, we have seen that little is known of the past hominin diet, especially during the Early Paleolithic. The diet of Late Pliocene and Early Pleistocene hominins was probably more diverse and less carnivorous than thought. Indeed, evidence of butchery is scarce and mostly based on a very small number of remains with some questionable cut marks (Domínguez-Rodrigo et al., 2010; McPherron et al., 2010, 2021; Sahle et al., 2017; Toth, 2017; Domínguez-Rodrigo and Baquedano, 2018).

The Problem of Applying Anatomical and Energetic Data From Extant Primates to Ancient Hominins

A higher-quality diet (and for example meat consumption) is often linked to an increase in brain size and a decrease in posterior tooth size (Aiello and Wheeler, 1995; Aiello and Wells, 2002; Snodgrass et al., 2009; Ungar, 2012). Improvements in dietary quality probably played an important role in brain expansion during the course of human evolution, but cannot alone explain why hominin brains grew (Leonard et al., 2011). Therefore, it is important to note that the measurement of the whole brain could be a poor proxy. Indeed, some more specific brain regions are more precisely related to feeding ecology, in particular to dietary quality, than the whole brain (DeCasien and Higham, 2019; Louail et al., 2019).

The reduction in molar size in *H. erectus*, Neanderthals and modern humans can be explained by a shorter chewing time owing to non-thermal food processing or cooking methods rather than by the rate of craniodental and body size evolution (Organ et al., 2011). This assumption is based on molar size (M2) and body mass. Firstly, we must be cautious about estimating body mass. Indeed, its inference in hominins takes into account the length of lower limb bones based on data from non-human primates. However, it is very difficult to associate isolated lower limb bones with skulls (from which species are determined), especially when different species are in the same spatio-chronological setting, as for example in the Turkana Basin during the Early Pleistocene (*Paranthropus boisei*, *H. ergaster*, *H. habilis,* and *H. rudolfensis*). Furthermore, the scenario is often only based on a few individuals, and does not consider the range variation of past populations. Secondly, the use of M2 size alone does not consider molar proportion variation across the dental arch, hominin species with a small overall dental size, and disproportionally highlights M2s and M3s. Furthermore, it has been shown that brain enlargement and dental reduction were decoupled and evolved at different rates (Gómez-Robles et al., 2017).

Moreover, the morphology of the masticatory system, in particular dentition, does not represent the diet, but reflects what individuals were able to eat rather than what they ate. This is Liem's paradox (Liem, 1980), of which *Paranthropus* is a good illustration, with its apparent ambiguity between anatomy and diet.

With regard to energetics, some researchers have proposed models to investigate hominin energy requirements, based on activity patterns, body mass and life history data from extant primates, with inferences based on hominin body mass. However, as mentioned in the previous paragraph, extreme caution should be taken with this proxy. For example, it has been estimated that the daily energy expenditure (DEE) of a *H. erectus* female was 2,086 kilocalories per day, 2,269 during gestation and 2,487 during lactation (Aiello and Key, 2002), and that she had to chew raw meat for 5.7–6.2 h/day to satisfy her energetic needs (Wrangham and Conklin-Brittain, 2003). However, according to Simmen et al. (2021) DEE increased with the augmentation of the resting metabolic rate, but life-history variables (maximum lifespan, gestation and lactation duration, interbirth interval, litter mass, age of first reproduction) would not be correlated with DEE after controlling for body mass and phylogeny. In the same way, Pontzer et al. (2012) stressed that the DEE seems to be more related to body size, age and sex than to cultural differences. The similarity of the DEE in hunter-gatherers and sedentary Westerners suggests that even our strong differences in lifestyle only produce a minor effect, and differences between populations result mainly from energy intake rather than expenditure (Pontzer et al., 2012). It should also be noted that the total DEE is measured outside a laboratory using the doubly labeled water method on extant primates in free-living conditions (Pontzer, 2017; Simmen et al., 2021), which of course, cannot be applied to extinct hominins. Therefore, most estimations of daily energy cost should be used with caution.

The Silent Part of Culture and Symbolism

While human behavioral ecology models are useful to predict which resource is edible and suitable or not in the diet, when a potential resource is not consumed, it may be a question of tradition, for example, totems or taboos, or of non-foraging activities, such as childcare or reproduction. Indeed, we have to keep in mind that other goals, and not only calorific return may prevail in diet choices, such as the acquisition of fat, vitamins, minerals or non-food products like pelts, bone tools or ornaments. For example, to date, a dozen European Middle Paleolithic sites have yielded evidence of the use of large raptor phalanges as personal ornaments or for symbolic purposes by Neanderthals (Morin and Laroulandie, 2012; Laroulandie et al., 2016; Rodríguez-Hidalgo et al., 2019). Others showed evidence of intentional feather removal, proffering another type of explanation for the Neanderthal exploitation of raptors (Peresani et al., 2011). Thus, we may ask what really governed forager's subsistence strategies in the past. Was it acquisition circumstances and the energetic return rate, as assumed by ecological approaches, or cultural and symbolic representations of animals, which is very difficult to assess for past societies. In reality, both probably played their part (Blasco et al., 2019b; Barkai, 2020). The role of culture and symbolism in food choices should of course not be overlooked. Far from being restricted to so-called "complex" societies, the eminently cultural nature of food is indeed a feature common to all human societies (Lévi-Strauss, 1964). Thus, choosing the appropriate food does indeed depend to a large extent on the available techniques and resources, but also on cultural and symbolic parameters. For example, in the case of the elephant, considerations other than the energetic return rate can motivate big game hunting, such as maintaining social position (Lupo and Schmitt, 2016). The development of ethnoarchaeological approaches through the 1970s and 1980s provided insights into these socio-cultural, but also technological aspects (Leroi-Gourhan and Brézillon, 1972; Yellen, 1977; Binford, 1978, 1980; Gallay, 1980). But this type of approach calls for caution. Indeed, when using current data from ethnology, we have to overcome the inherent biases of ethnoarchaeology, i.e., a too strict and direct analogism and the determinism that this may imply (Lévi-Strauss, 1952; Cleuziou, 1984).

In any case, for the Paleolithic, the social and symbolic dimension of food is unfortunately particularly difficult to approach (see Costamagno and Daujeard, 2021). Nevertheless, some recent studies show that the marks left by marrow extraction can highlight the existence of traditional butchery practices specific to certain Middle and Late Paleolithic groups of hunter-gatherers (Blasco et al., 2013; Masset et al., 2016; Vettese et al., 2017). It has been also been suggested for example that the intense disarticulation and fragmentation of phalanges and short bones in the European Middle Magdalenian, may reflect ritualized butchery practices, in connection with the relationships maintained between Paleolithic people and their game (Birouste, 2020). These works extend slightly beyond the strictly economic character to which the diet of our Paleolithic ancestors is generally reduced in zooarcheological studies.

Finally, we must be aware that in applying HBE to Archeology, it is necessary to contextualize data according to palimpsest biases, using geoarchaeology, refitting, seasonal data, spatial analyses, etc., in order to obtain the best time resolution. We also have to keep in mind that a whole section is missing from our understanding of animal acquisition choices among past societies, i.e., cultural and symbolic representations, which explain a large part of the relationships we have with nature, if not all (Descola, 2005).

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CD and SP wrote the body of the manuscript. Both authors contributed to the article and approved the submitted version.

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Think Fast!: Vervet Monkeys Assess the Risk of Being Displaced by a Dominant Competitor When Making Foraging Decisions

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Foraging animals need to quickly assess the costs and benefits of different foraging decisions, including resource quantity, quality, preference, ease of access, dispersion, distance, and predation risk. Social animals also need to take social context into account and adapt foraging strategies that maximize net resource intake and minimize contest competition with conspecifics. We used an experimental approach to investigate how social context impacts wild vervet monkey (*Chlorocebus pygerythrus*) foraging decisions in a multi-destination pentagon array. We baited four platforms with less-preferred corn and one platform with a larger, preferred resource (half banana) that required handling time. We ran over 1,000 trials and found that when monkeys foraged alone, they usually took the path that minimized travel distance but prioritized the preferred-food platform when in competition. However, the foraging strategy chosen by low-ranking individuals depended on the handling skill of the decision maker (i.e., time it would take them to retrieve the banana), the relative rank of their audience members (i.e., who has priority-of-access to resources), and the distance audience members were from the experiment site (i.e., their travel time). When the risk of being displaced by a dominant competitor was low (because they were far away and/or because the decision-maker was skilled in retrieving the banana), low-ranking individuals chose a route that minimized travel costs. Conversely, when the risk of losing food to a dominant competitor was high, decision-makers rushed for the preferred-food platform at the onset of the trial. When the risk of displacement was moderate because a dominant audience member was at least 50 m away, low-ranking individuals partly prioritized the preferred-food platform but took the time to stop for one platform of corn on the way. This strategy increased the total amount of food obtained during the trial. These findings suggest that lower-ranking individuals, who experienced high contest competition at the foraging experiment, calculated the risk of being displaced by a dominant competitor when making foraging decisions. This experiment demonstrates that vervets go through a complex decision-making process that simultaneously considers the profitability of different foraging decisions and their social context.

Keywords: distance optimization, optimal foraging theory, multi-destination array, decision making, social context, foraging experiment, handling time, dominance rank

INTRODUCTION

Since optimal foraging theory was first proposed more than 50 years ago (MacArthur and Pianka, 1966), behavioral ecologists have dedicated immense effort in understanding how animals optimize resource intake. Foraging individuals may consider resource quantity, quality, preference, ease of access, dispersion, distance, visibility, predation risk, and the level of competition (Croy and Hughes, 1991; Menzel, 1997; Giraldeau and Caraco, 2000; Stephens et al., 2007; Menzel et al., 2008; Fortin and Fortin, 2009; Marshall et al., 2012; Sayers and Menzel, 2012; Teichroeb and Aguado, 2016; Kumpan et al., 2019). The profitability of a given food item is typically framed as energy gained divided by pursuit plus handling time (Pyke, 1984; Stephens and Krebs, 1986). Thus, profitability increases considerably as pursuit and handling time approach zero, leading to strong selection pressure to decrease the costs of these two factors, if possible (e.g., Anholt et al., 1987; Stillman et al., 2000; Catania and Remple, 2005; Cooper and Anderson, 2006; Paredes et al., 2015; Wilson et al., 2015). Pursuit often equates to the distance needed to travel to get to a food site (Janson, 2000, 2007). Handling time is typically manual processing of food items to remove the edible portion or processing the food in the mouth before swallowing (Isbell et al., 1998; Cadieu et al., 2008; Gunst et al., 2010; Sayers and Menzel, 2012); both of which reduce the intake of new food items. The energy spent in pursuit selects for cognitive abilities to remember the location of food patches and their characteristics, determining a route that will minimize travel costs and remembering how visual distance to rewards relates to travel time (Shettleworth, 2010; Janmaat et al., 2014). While handling time may be a key selective pressure for social learning as food extraction and manipulation skills are often transmitted socially (Whiten and Mesoudi, 2008; Reader and Biro, 2010; Thornton and Clutton-Brock, 2011).

In gregarious animals, social context can also impact decision making because group members are potentially competitors for important resources like food or mates (Bugnyar and Heinrich, 2005; Dally et al., 2006; Rosati and Hare, 2012; Teichroeb and Aguado, 2016). In primates, within-group contest competition for food items can be intense, imposing costs on animals such as being displaced at feeding sites and potentially leading to the risk of injury or even death (Wrangham, 1981; Janson, 1985; Vogel, 2005; Kumpan et al., 2019). Contest (or interference) competition arises when limiting resources are clumped and defensible and direct conflict occurs over which individuals control them (Nicholson, 1954; Janson and van Schaik, 1988), which often leads to the formation of dominance hierarchies (Shively, 1985). While dominance hierarchies decrease the need to engage in contest competition, contest competition still occurs. Consequently, a comprehensive understanding of foraging behavior in gregarious animals can only be built if we investigate how decision-makers modify their behavior in the face of competition.

Research in a number of species shows that foragers modify their behavior when in competition. For example, studies conducted on various herbivores have found that foraging individuals increase their intake rates as the number of potential competitors present increases (Molvar and Bowyer, 1994; Fritz and de Garine-Wichatitsky, 1996; Shrader et al., 2006). Similarly, vervet monkeys (*Chlorocebus pygerythrus*) choose paths that minimize travel distance when foraging alone, but prioritize high-reward sites when competitors are present (Teichroeb and Aguado, 2016). Furthermore, other studies suggest that foraging decisions are not only based on whether an individual is currently competing with a conspecific, but that decision makers also assess the likelihood of losing food to a competitor. For example, when deciding whether to try and access a food patch, subordinate pigs (*Sus scrofa*) use the location and movement trajectory of a dominant competitor to determine whether they will be able to arrive at the patch ahead of the competitor (Held et al., 2002). Ravens (*Corvus corax*) consider the visual perspective of conspecifics to differentiate between knowledgeable and ignorant competitors (Bugnyar and Heinrich, 2005), and both California scrub-jays (*Aphelocoma californica*) and Eurasian jays (*Garrulus glandarius*) selectively cached food that audience members were least motivated to steal (Ostojić et al., 2017).

The goal of this study was to examine how social context impacted route choice in a social primate, the vervet monkey. We have been using carefully designed foraging experiments with high trial sample sizes to understand how this species solves multi-destination routes (Teichroeb, 2015; Teichroeb and Smeltzer, 2018) and makes multifactor foraging decisions (Teichroeb and Aguado, 2016; Kumpan et al., 2019). Because vervets will leave their foraging group to visit the experiment site alone, but will also participate when surrounded by group members, this experimental paradigm is also ideal for examining how social context impacts foraging decisions. Since our previous work has shown that foraging vervet monkeys modify their route choice when a competitor is present (Teichroeb and Aguado, 2016), this study focused on investigating how the risk of contest competition impacted foraging decisions.

To facilitate comparisons with our previous work (Teichroeb and Aguado, 2016; Kumpan et al., 2019), we used the same pentagon-shaped foraging array with platforms (i.e., food patches) five meters apart (Lihoreau et al., 2011). In this array, the most efficient path is to start with the nearest platform and move around the outside of the array as this route minimizes travel distance (**Figure 1**; ESM 1). We baited four platforms in the pentagon with less-preferred corn kernels and one platform was randomly chosen in each trial to contain a larger, preferred reward with high handling time (i.e., a half-banana in an unopenable box with a small hole cut in the top). This box required the monkeys to manipulate it (e.g., tip, roll, shake) to retrieve the banana, and so mimicked the handling costs that this species often faces when feeding on natural food items (Isbell and Young, 1993). Importantly, food resources with high handling times elicit frequent contest competition (Sirot, 2000; Korstjens et al., 2002; Marshall et al., 2012; Wikberg et al., 2013), and have a high risk of kleptoparasitism (Steele and Hockey, 1995; Broom and Ruxton, 2003), because the time spent handling gives competitors time to try and obtain the food item. Therefore, by imposing high handling time on the preferred food, we increased the risk that an audience member

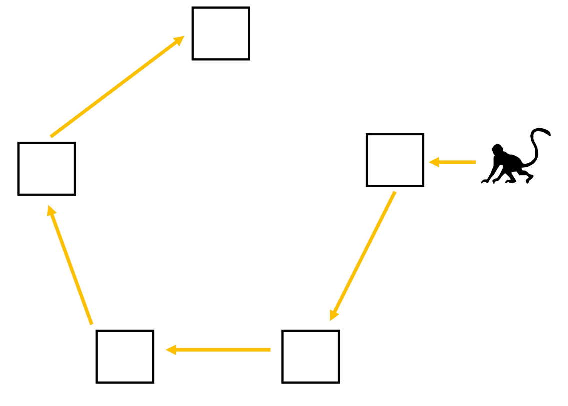

FIGURE 1 | Travel path that minimizes travel distance if visiting all food patches in a pentagon-shaped foraging array.

would be able to travel to the experiment site and take priority-of-access to the preferred-food/high-handling time platform (hereafter "preferred-food platform") or steal the food item from the handling individual. By imposing high handling time on the preferred-food reward, we increased the risk that lower-ranked and/or unskilled individuals would lose this preferred-food reward to an audience member. To investigate whether the risk of contest competition impacts the decision-making process, we considered both the forager's speed in retrieving the banana from the box (i.e., their handling skill, where as individuals got more experienced and skilled, handling time decreased) and the composition and location of their audience. Not all audience members are equally likely/able to displace a group member at a food resource. Subordinate audience members cannot take priority-of-access to contested resources, and audience members who are too far away will have long travel times to reach the experiment site.

We always endeavored to place the preferred-food reward so that it was not on the decision-makers nearest platform. This was accomplished by placing the preferred-food reward on a platform that was not the nearest to any individual present at the experiment site, or when this was not possible because there were many monkeys present, to avoid placing it near high-ranking individuals or individuals that had recently been participating in the experiment. By placing the preferred-food reward more than one platform away from likely participants, we ensured that decision-makers had to choose between starting with their nearest platform or eating their preferred food first. In our analyses, we examine the factors that impacted the first two decisions the focal monkey made in each trial (**Figure 2**); which platform to visit first (i.e., Decision 1) and which platform to visit second (i.e., Decision 2). This approach allowed us to investigate the extent to which monkeys prioritized their preferred-food platform, vs. chose the nearest one or two platforms of corn. With this approach we were able to identify three distinct strategies used by the vervets (**Figure 2**). The first strategy was to rush for the banana at the onset of the trial (**Figures 2A,G**; ESM 2, 3), "prioritizing the preferred-food platform." The second was to stop for "one platform of corn en route to their preferred food" (**Figures 2D,I**; ESM 4). This intermediate strategy still prioritized the banana but ensured the focal monkey was able to obtain at least one platform of corn before competitor(s) arrived (and ate corn while they themselves handled the box). The third strategy was to take the route that would "minimize travel distance" if visiting all five platforms (**Figure 1**; ESM 1), by starting at the nearest platform and then continuing to next corn platform encountered when moving around the outside of the array (**Figure 2J**; ESM 5). Individuals selecting their two nearest platforms of corn could be doing so because (1) they were unwilling to try and obtain the preferred food-reward, or (2) they planned to visit the preferred-food platform when it was encountered along this shortest-distance path (**Figure 1**). In either case, starting with the two nearest platforms of corn would minimize the distance travelled compared to selecting corn platforms further away.

Given our previous findings (Teichroeb and Aguado, 2016), we expected that solitarily foraging vervets, who are able to obtain the food rewards on all five platforms, should forage efficiently by minimizing travel distance as they move through the array (**Figures 1**, **2E,J**). Alternative routes would involve cutting across the array and then back-tracking, increasing travel costs. Conversely, monkeys in competition were predicted to assess the risk of contest competition, and prioritize the preferred-food platform when the risk of being displaced by a dominant competitor was high. Although females can be dominant to males in this species (Young et al., 2017; Hemelrijk et al., 2020; Li et al., 2021), all adult males were dominant to all other group members during the time of this study. Therefore, we expected that adult males would be less vulnerable to contest competition than the other age-sex classes that participated in the experiment, and so would show a greater propensity to minimize travel distance rather than prioritizing the preferred-food platform. Hence, we expected them to visit their two nearest corn platforms first, and obtain the preferred food-reward as it was encountered. Conversely, we expected that adult females, subadult males, and subadult females would be more likely to bypass less preferred corn platforms and rush to retrieve the banana from the box. Furthermore, we expected these lower-ranked individuals to be more likely to prioritize the preferred-food platform when their audience contained group members that out-ranked them, particularly when dominant individuals were relatively close to the experiment (i.e., had short travel times and could approach the array and displace subordinates). Lastly, we expected that handling skill would modify route choice, with proficient monkeys showing a lower propensity to prioritize the preferred-food platform. Speed in retrieving the banana from the box should give decision makers extra time to consume corn before visiting the preferred-food platform, maximizing the total food rewards obtained.

MATERIALS AND METHODS

Study Site and Animals

This research was carried out at Lake Nabugabo, Masaka District, central Uganda (0°22′-12°S, 31°54′E). Lake Nabugabo

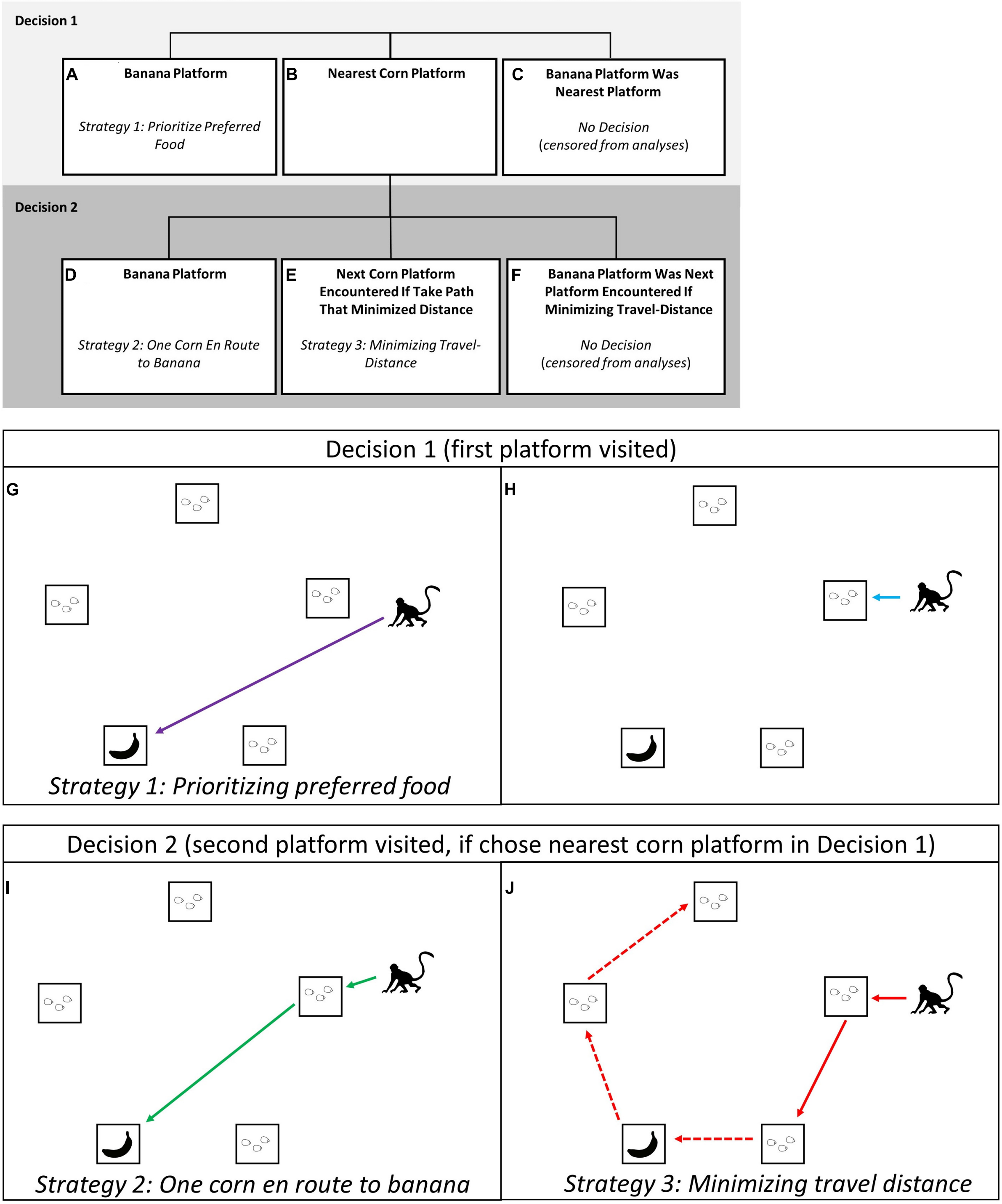

FIGURE 2 | Within this multi-destination foraging experiment, vervet monkeys at Nabugabo, Uganda needed to make two decisions: which platform to visit first [Decision 1: **(A,B,G,H)**, and which to visit second, Decision 2: **(D,E,I,J)**]. Decision 1 was a choice between rushing for the platform with the banana **(A,G)**, a strategy which prioritized the preferred-food platform, or **(B,H)** to start at the nearest corn platform. We attempted to bait platforms such that the preferred food (banana) was not the nearest platform; trials in which the banana was on the nearest platform were censored from the analysis because these trials did not require the monkey to choose between minimizing travel distance and prioritizing preferred food **(C)**. Individuals who chose to visit their nearest corn platform first could then decide if they wanted to **(D,I)** proceed immediately afterward to the preferred-food platform, or **(E,J)** travel around the pentagon array in a trajectory that would minimize travel distance, getting the preferred-food when they came to it. Trials in which the platforms were baited such that the preferred-food platform was the second platform encountered when taking the path that minimized travel distance **(F)** were censored from the analyses because monkeys in these trials did not have to choose between the platform with their preferred food and minimizing travel distance. Note: in box **(J)** we use the dashed arrow to show the route that a monkey foraging efficiently was expected to take, however, they may not have obtained the rewards on all five platforms if in competition.

is a small lake (8.2 × 5 km^2) located on the western edge of Lake Victoria at an elevation of 1,136 m. Our research station is on the western side of Lake Nabugabo, in an area of mixed primary and secondary forest fragments, wetland, farmer's fields, and tourist camps (Chapman et al., 2016). The study subjects were a habituated group of vervet monkeys (*Chlorocebus pygerythrus*) referred to as K group, which had been followed continuously since 2016 and had previously participated in a foraging experiment (Kumpan et al., 2019). All individuals were identifiable by their natural markings. At the time of the study, the group contained 38–44 individuals (4–7 adult males, 10 adult females, 3 subadult males, 5 subadult females, 16–19 juveniles and infants).

Experimental Design

This experiment was conducted from January to April 2019. We arranged five wooden platforms (wooden tables, 0.75 m high, with a square flat top 0.75 m × 0.75 m) in a pentagon array with a distance of 5 m between each platform (**Figure 1**; as in: Teichroeb and Aguado, 2016; Kumpan et al., 2019). The array was placed in a relatively open area among frequently visited feeding patches for K group, so that we could also record accurate data on the distance of approaching competitors and which individuals were in the audience along with their approximate distance. Similarly, by conducting the experiment in the open, any monkeys present within approximately 100 m of the experiment site could also see the array, the location of the different food rewards, and potential competitors.

We first ran two-choice experimental preference trials to verify that the vervets preferred the banana over the dried corn. All five individuals tested chose banana over corn in the quantities the platforms were baited with. After preferences were determined, we baited the platforms on each trial as follows: four platforms were baited with three kernels of the less-preferred dried corn (soaked in boiling water to soften it) and one platform was baited with the preferred banana in an unopenable, plastic, rectangular box with a small hole cut in the top on one side (**Figure 3A**). Because the sides of the box were transparent, the half banana was visible inside of the box. Handling times varied from 1 s to 69 s, with the average observed handling time being 6.7 s. The platform where the box was located was randomized each trial, but we avoided placing it on the platform nearest to any of the monkeys that were present at the experiment site. Thus, the monkeys usually had to choose between their nearest platform containing corn and the preferred-food platform at a greater distance. The first monkey to feed at a platform was deemed the "focal" and any subsequent individuals "competitors." The behavior of the monkeys in the array was video recorded on each trial with narration by TJA-R and later these data were coded into Microsoft Excel by TJA-R, EV, and KA. During trials, we recorded which platform contained the preferred-food/high-handling time target (i.e., the banana in the box), the number of animals participating and their identities, the composition of the audience and the distance of these individuals (e.g., < 25 m, 26–50 m, 51–75 m, 76–100 m, > 100 m/out-of-sight), the order of platform visitation, which individual received the rewards on each platform, the duration of handling time (i.e., time spent manipulating the box to get the banana out, **Figure 3B**), and any social interactions that occurred. The proximity of audience members to the experiment site was recorded in distance categories because it was not feasible to collect more precise distance estimates for all group members within 100 m.

The social interactions that occurred around the foraging experiment, as well as ongoing behavioral data collection, allowed us to determine the dominance hierarchy for K group. There was a lot of flux in dominance relationships at the time of the experiment due to new male immigration and dominance challenges among some of the females. We therefore chose to use Elo-ratings (Elo, 1961, 1978; Albers and de Vries, 2001; Neumann et al., 2011) to quantify both the focal's rank, and whether they had higher-ranking audience members. We used the known ordinal ranks at the onset of the experiment, determined using the long-term behavioral data collected at the study site, as the "startvalue" when estimating Elo-ratings. Decided dyadic contests that were observed throughout the study period were used to calculate the Elo-rating for each group member on each day. These Elo-ratings were used as the "focal's rank" in our models, and we also used the daily Elo-ratings to determine if the focal was higher vs. lower-ranking than each group member present in their audience. We then coded the distance to the nearest higher-ranking audience member. Elo-ratings were calculated using the "EloRating" package (version 0.46.11, Neumann and Kulik, 2020) in R (version 3.6, R Core Team, 2019).

Data Analyses

We used generalized linear mixed models (GLMMs) to examine the frequency that the age-sex classes (adult males vs. adult females and subadults) selected different food rewards in Decision 1 and Decision 2. We used four GLMMs to assess the factors that impacted vervet decision-making in this foraging experiment: adult male choices in Decision 1, adult female/subadult choices in Decision 2, adult male choices in Decision 2, and adult female/subadult choices in Decision 2. Because all adult males were dominant to all other group members during the study period, and because adult males rarely approached the experimental site at the same time as other adult males, adult males were rarely focal individuals when there was a dominant competitor present. Thus, adult males experienced very little contest competition when participating in the foraging experiment and were unlikely to lose food to a dominant competitor. Consequently, we expected adult males to go through a different decision-making process, and so we modeled adult males separately from adult females, subadult males, and subadult females. Juveniles were not able to gain access to the foraging experiment and so were not included in this study.

In each GLMM we included individual ID as a random effect to control for repeated observations of individuals (pseudo replication) (Zuur et al., 2009). We did not include random slopes as the data did not support the more complex model structure (Bates et al., 2015a; Matuschek et al., 2017; Harrison et al., 2018). We censored any individual with less than 10 trials from our analyses. We also censored any trials in which the focal accessed a food reward before all the platforms were baited, because in

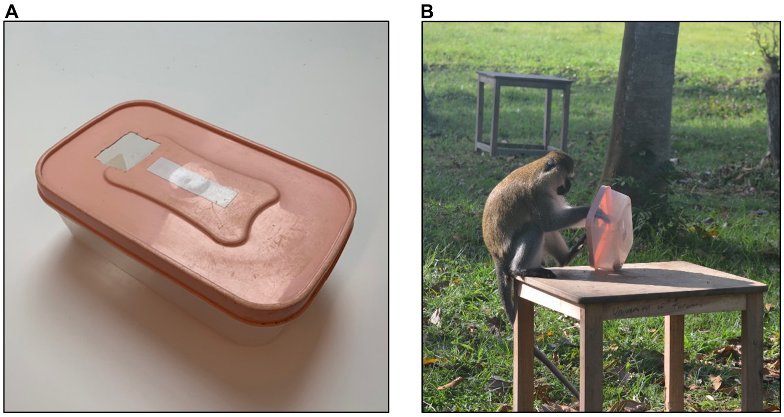

FIGURE 3 | The preferred-food/high-handling time platform contained **(A)** a plastic box with a hole cut in the top, which could not be opened, with a half banana inside. **(B)** Individuals had to manipulate the box to get the banana out and this was recorded as their handling time [Photo credits: **(A)** JT, **(B)** TJA-R].

such cases, the platform they choose to visit first may have been impacted by the presence/location/movement of the observer. The response variable in the Decision 1 models was whether the focal monkey chose the preferred-food platform (i.e., a strategy of strongly prioritizing the banana), vs. their nearest corn platform (**Figure 2**). In the Decision 2 models, the response variable was whether the focal visited the preferred-food platform second (i.e., a one corn en route to the banana strategy, prioritizing the banana to a lesser extent) vs. the next corn platform (i.e., a route that minimized travel distance if visiting all five platforms) (**Figure 2**). Because both of these response variables are dichotomous, we set a binomial error structure and logit link function. We censored any Decision 1 trials in which the preferred-food reward was placed on the focal's nearest platform, as well as Decision 2 trials in which the preferred-food reward was on the next platform encountered if moving around the outside of the pentagon array (**Figures 2C,F**). We did so because in these trials, the focal did not have to choose between a route that would minimize travel distance (if visiting all five platforms) (**Figure 1**) and prioritizing the preferred-food reward (**Figures 2G,I**). We also censored trials in which the foraging strategy of the focal did not fit into the decision tree outlined in **Figure 1**. In total, we censored 18 trials (1.7% of the 1,046 Decision 1 trials) in which the focal did not choose either their nearest corn platform or the preferred-food platform when making Decision 1 (i.e., they visited a corn platform that was not their nearest), and 20 trials (3.9% of the 515 Decision 2 trials) in which the focal did not choose the next corn platform encountered or the preferred-food platform when making Decision 2 (i.e., they only visited one corn platform before being displaced by a dominant competitor or they fed at two corn platforms that were not the first and second platforms encountered).

Predictor variables included (1) the focal's dominance rank, (2) their handling skill, (3) whether they were foraging in competition, and (4) the risk of losing food rewards to a dominant competitor. We quantified dominance rank using the daily Elo-rating of the focal individual. Because individuals tended to decrease their handling time as they gained more experience handling the box (Arseneau-Robar, unpublished data), we used the focal's average handling time across their five most recent opportunities removing the banana from the box as an index of their current handling skill. We determined whether the focal had a competitor present at the onset of the trial if another group member (dominant or subordinate) was in close proximity to the platforms (<25 m) at the onset of the trial, and attempted to access the platforms by approaching a platform closely, jumping up onto it and/or feeding (i.e., whether the focal was foraging in competition). Lastly, we indexed the risk of losing food to a dominant competitor using the distance to the nearest dominant audience member. While all four of the predictor variables were included in adult female/subadult models, the variable "distance to the nearest dominant audience member" was not included in the adult-male models (i.e., the adult male models only included rank, recent handling time, and whether the focal was foraging in competition as predictors). This was done because, unlike the other age-sex classes, adult males rarely had a dominant audience member (**Figure 4**) because no group members out-ranked the alpha male and so one of the seven adult males included in this study could never have a dominant audience member. Additionally, subordinate males rarely had a dominant audience member because the low levels of male-male tolerance in vervet monkeys meant that low-ranking adult males typically waited for higher-ranking adult males to lose interest in the platforms and leave the area before they approached the experiment site. The lack of trials in which adult males had dominant audience members (**Figure 4**) created unbalanced models that failed to converge, and so we removed this predictor variable to improve model performance.

All analyses were conducted in R (version 3.6, R Core Team, 2019). We used the "car" package (version 3.0-7, Fox and Weisberg, 2019) to calculate variance inflation factors (VIF). These were all low (<3) and pairwise correlation coefficients were all well below 0.8, indicating there was no multicollinearity among predictors (Zuur et al., 2009; Field et al., 2012). We assessed model stability by using the "influence.ME" package (version 0.9-9, Nieuwenhuis et al., 2012) to calculate Cook's

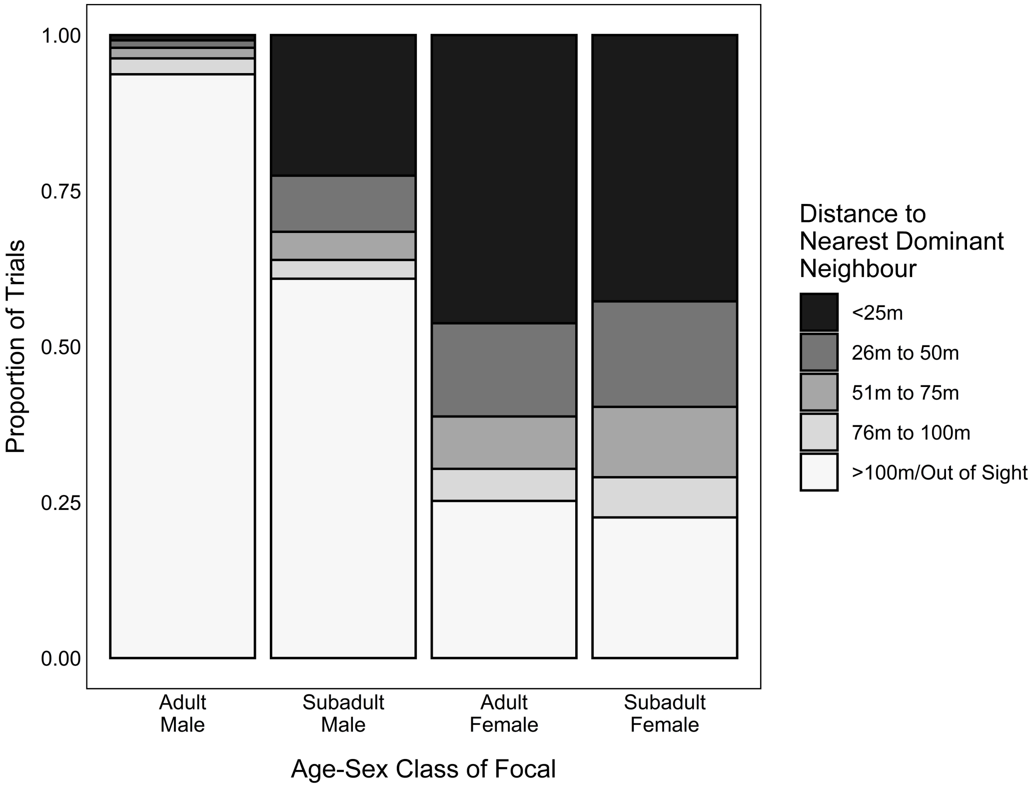

FIGURE 4 | Proportion of trials where the distance to the nearest dominant neighbor was within 25 m, 26–50 m, 51–75 m, 76–100 m or > 100 m/out of sight, for each age-sex class that participated in the foraging experiment.

distances and DFBeta values. Both Cook's distance values and DFBeta values were concerningly high (Belsley et al., 2004; Field et al., 2012) for one male (i.e., level of the random effect) in the adult male Decision 2 model, and removing this influential case impacted the fixed effects that were significant in this model. Therefore, we have presented the model output from both the full and reduced datasets. We used the "lme4" package (version 1.1-21, Bates et al., 2015b) to build GLMMs, and the "DHARMa" package (version 0.3.3.0, Hartig, 2021) to check for over- or under-dispersion. For the distance to nearest dominant audience member variable, we set "> 100 m/out-of-sight" as the reference category, and compared the other factor levels to it. We assessed the significance of predictor variables using 95% profile confidence intervals (lme4, version 1.1-21, Bates et al., 2015b), and the overall fit of each GLMM using a likelihood ratio test to compare the full model to the null model, which included the intercept and random effects. Lastly, we used the "MuMIn" package (version 1.43.17, Bartoń, 2020) to estimate the total variance explained [delta $R^2_{GLMM(c)}$] by each model (Nakagawa and Schielzeth, 2013).

RESULTS

In this experiment, three main foraging strategies were exhibited by the vervet monkeys: rushing for the platform with the banana at the onset of the trial (i.e., prioritizing their preferred food), the intermediate strategy of stopping for one platform of corn en route to the preferred-food platform, and taking the route that minimized travel distance if visiting all five platforms (**Figure 2**). These three strategies accounted for the choices that decision-makers made in the majority of trials (98% of trials in Decision 1 and 96% of trials in Decision 2). Of the 1,028 trials in which we were able to assess Decision 1, the monkeys prioritized the preferred-food platform in 22% of cases. When the focal monkey visited their nearest corn platform first, and the preferred-food platform was not the next platform encountered if minimizing travel distance (Decision 2), the focal typically displayed one of the two following patterns of behavior. They could still prioritize the preferred-food platform but take the time to obtain one platform of corn on the way (i.e., a one corn platform en route to the banana), or they could visit the next corn platform encountered if taking the path that minimized travel costs. The monkeys used the one corn en route strategy in 23% of $N = 495$ trials and chose the next corn platform encountered in 77% of trials. When individuals visited the next corn platform encountered second (i.e., the solid arrows in **Figure 2J**), they continued on to the preferred-food platform in 91% of cases (i.e., the dotted arrows in **Figure 2J**), indicating that the "minimizing travel distance" strategy predominantly reflected a plan to visit the preferred-food platform when it was encountered (ESM 1,5), not that the focal was unwilling to try and obtain the preferred food-reward. Overall, focal individuals obtained the banana in 93% of trials, showing that their foraging strategies were typically effective in ensuring they gained access to their preferred food-reward. Focals were most likely to lose the preferred-food rewards to a competitor when exhibiting the minimizing travel distance strategy (banana lost in 7.7% of trials), and were least likely to lose the preferred-food reward when they rushed for the food patch containing the banana at the onset of the trial (2.2% of trials Strategy 1 was exhibited).

Whether or not the focal monkey was foraging in competition [i.e., competitor(s) were actively approaching the array or were within it] impacted the propensity to prioritize the platform with the preferred food. Of the $N = 818$ trials in which the preferred-food reward was 2 platforms away from the nearest platform (i.e., the trials included in the Decision 2 analyses), decision-makers prioritized the preferred-food reward by rushing for it at the onset of the trial in 56% of trials in which they were in competition from the onset ($N = 422$), but only 22% of the trials in which they were not in direct competition ($N = 396$). Conversely, decision-makers exhibited the minimizing travel distance strategy in only 28% of the trials in which they were competition, but 66% of the trials in which they started the trial foraging alone. The one corn en route to the preferred reward strategy was utilized in 16% of trials when in competition, and 12% of trials where no competitor was present at the onset of the trial.

Adult males prioritized the preferred-food by rushing for the banana at the onset of the trial in only 12% of trials. Conversely, when the focal was an adult female, subadult male or subadult female, they visited the preferred-food platform first in 35% of trials (**Figure 5A**). This difference, however, was not statistically significant (GLMM: $N = 1{,}028$, $z = -0.868$, $P = 0.385$). The only factor that influenced the propensity for adult males to prioritize the preferred-food platform was whether or not they made Decision 1 in the presence of a competitor (**Table 1**); however, this trend was not statistically significant. Furthermore, the poor performance of the adult-male/Decision 1 model compared to the null model (Likelihood ratio test: $N = 572$, $X^2 = 4.69$, $P = 0.196$) suggests that the presence of a competitor did not have a consistent impact on their initial platform choice.

The age-sex classes that were low-ranking (i.e., adult females and subadults) were significantly more likely to prioritize the preferred-food platform if they were still inefficient at retrieving the banana from the box (i.e., their five most recent handling times were relatively long) (**Table 1**; ESM 2). We also found having a dominant group member 26–50 m away (**Table 1**; ESM 3), relative to the reference category (>100 m/out-of-sight), to have a significant impact on the initial platform choice of females/subadults, indicating that females/subadults were more likely to prioritize the preferred-food platform when there was a risk of being displaced by a dominant competitor. Adult females and subadults also showed a strong propensity to weigh the risk of contest competition when making Decision 2. We found that adult females/subadults were significantly more likely to visit the preferred-food platform second (i.e., do one corn platform en route to the banana instead of minimizing travel distance) when they had a dominant audience member 51–75 m away, than when there were no higher-ranking group members within 100 m/in sight (**Table 2**; ESM 4). That females/subadults choose the preferred-food platform first when there was a dominant competitor 26–50 m away, and were more likely to select it second when there was a dominant competitor 51–75 m away, suggests that the monkeys consider not only the relative rank of their audience members, but the travel time it would take potential competitors to arrive at the experiment site. Handling skill did not impact second platform choice in females/subadults, but they were more likely to prioritize the preferred-food reward if a competitor was present (**Table 2**).

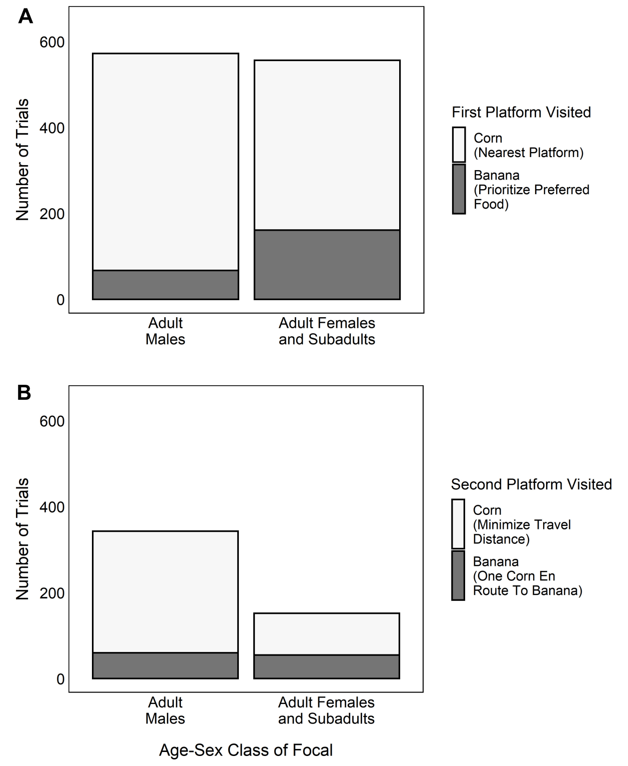

FIGURE 5 | The number of trials in which adult males and adult females/subadults each chose different food rewards when making **(A)** Decision 1 (i.e., which platform to visit first), and **(B)** Decision 2 (i.e., which platform to visit second, if they had chosen their nearest corn platform in Decision 1).

Adult males were more likely to select the preferred-food platform second (i.e., do one corn en route to the banana) in trials where they were in competition (**Table 2**). However, overall adult males were significantly less likely to employ a one corn en route to the banana strategy than were adult females/subadults (GLMM: $N = 495$, $z = -2.43$, $P = 0.015$; **Figure 5B**). Of the trials in which they selected their nearest corn platform for Decision 1, adult males chose to minimize travel distance in 83% of trials and do one corn en route to the banana in 18% of trials (**Figure 5B**). Adult females and subadults used the one corn en route to the banana strategy in 36% of cases (**Figure 5B**). Lastly, we found that rank influenced Decision 2 for adult males, with higher-ranking males being more likely to do one corn en route to the

TABLE 1 | Likelihood the first platform the focal individual visited (Decision 1) was the one containing the preferred-food/high-handling time food reward (i.e., the banana in a box that necessitated handling).

	B	SE	*z*	*P*	Lower CI	Upper CI
Adult Males						
Intercept	−2.65	0.68	–	–	–	–
Rank	0.42	0.50	0.84	0.399	−0.51	1.57
Recent Handling Time	0.11	0.18	0.59	0.554	−0.27	0.44
Foraging in Competition	*0.55*	*0.31*	*1.80*	*0.073*	*−0.06*	*1.16*
Adult Females and Subadults						
Intercept	−2.00	0.84	–	–	–	–
Rank	0.93	0.62	1.50	0.133	−0.24	2.37
Recent Handling Time	**0.34**	**0.14**	**2.42**	**0.016**	**0.07**	**0.63**
Foraging in Competition	0.33	0.39	0.86	0.391	−0.45	1.12
Nearest Dominant Individual:						
≤ 25 m	−0.33	0.41	−0.81	0.419	−1.17	0.48
26–50 m	**0.97**	**0.44**	**2.19**	**0.028**	**0.08**	**1.88**
51–75 m	−0.30	0.52	−0.57	0.566	−1.36	0.72
76–100 m	0.58	0.79	0.74	0.460	−0.97	2.20
> 100 m/Out of Sight	–	–	–	–	–	–

Significant fixed effects are bolded and trends are italicized. The adult male model did not perform significantly better than the null model, which contained only the intercept and random effects [Likelihood ratio test: N = 572, X^2 = 4.69, P = 0.196, delta $R^2_{GLMM(c)}$ = 0.27], however, the model for adult females and subadults did [Likelihood ratio test: N = 456, X^2 = 16.42, P = 0.022, delta $R^2_{GLMM(c)}$ = 0.61].

TABLE 2 | In cases where the focal individual had chosen their nearest corn platform in Decision 1, the likelihood that the second platform visited (Decision 2) was the preferred-food/high-handling time one (i.e., a "one corn en route to the banana" strategy) instead of the next corn platform encountered if minimizing travel distance (i.e., a "minimizing travel distance" strategy).

	B	SE	*z*	*P*	Lower CI	Upper CI
Adult Males (full dataset)						
Intercept	−2.43	0.42	–	–	–	–
Rank	**1.09**	**0.35**	**3.13**	**0.002**	**0.35**	**1.94**
Recent Handling Time	0.04	0.20	0.21	0.834	−0.39	0.41
Foraging in Competition	*0.66*	*0.37*	*1.81*	*0.070*	*−0.06*	*1.39*
Adult Males (influential male censored)						
Intercept	−2.73	0.33	–	–	–	–
Rank	0.12	0.32	0.37	0.71	−0.52	0.79
Recent Handling Time	0.08	0.21	0.38	0.70	−0.38	0.46
Foraging in Competition	*0.98*	*0.53*	*1.85*	*0.06*	*−0.10*	*2.01*
Adult Females and Subadults						
Intercept	−0.93	0.33	–	–	–	–
Rank	−0.03	0.22	−0.28	0.898	−0.46	0.51
Recent Handling Time	−0.23	0.20	−1.17	0.242	−0.65	0.14
Foraging in Competition	**0.95**	**0.47**	**2.02**	**0.043**	**0.03**	**1.90**
Nearest Dominant Individual:						
≤ 25 m	−0.19	0.49	−0.39	0.699	−1.18	0.75
26–50 m	−0.88	0.71	−1.24	0.216	−2.47	0.41
51–75 m	**1.85**	**0.66**	**2.79**	**0.005**	**0.59**	**3.24**
76–100 m	0.04	0.89	0.04	0.965	−1.98	1.70
> 100 m/Out of Sight	–	–	–	–	–	–

Trials in which the platform with the banana was the next platform encountered when minimizing travel distance were censored out of this analysis. We present the model for adult males using the full dataset, as well as when one influential male (i.e., one level of the random effect) was censored from the analysis. Significant fixed effects are bolded and trends are italicized. Both the full model for adult males [Likelihood ratio test: N = 343, X^2 = 12.41, P = 0.006, delta $R^2_{GLMM(c)}$ = 0.22], and the model for adult females and subadults [Likelihood ratio test: N = 152, X^2 = 15.52, P = 0.030, delta $R^2_{GLMM(c)}$ = 0.12] performed significantly better than the null model (model with only the intercept and random effects). The adult male model with the influential random-effect level censored did not outperform the null model [Likelihood ratio test: N = 272, X^2 = 4.82, P = 0.186, delta $R^2_{GLMM(c)}$ = 0.06].

banana than lower-ranking males (**Table 2**). However, this result was driven by the male who was the alpha male in the group for the majority of the study period. When he was censored from the analysis, we found no effect of rank on the propensity for adult males to use a one corn en route strategy. Adult males also showed a weak tendency to choose the platform with the preferred-food reward when making Decision 2 if they were foraging in competition (i.e., trend effect; **Table 2**).

DISCUSSION

The results from this study demonstrate that vervet monkeys adapt their foraging decisions, depending on their experience and the current social context, to maximize food intake and decrease costs. Consistent with previous studies (Teichroeb and Aguado, 2016), solitarily foraging vervets were more likely to forage efficiently, going through the array along the path that minimized travel distance, while monkeys foraging in competition [i.e., with competitor(s) in close proximity (<25 m) to the platforms and attempting to access food] were more likely to prioritize the preferred-food platform. Beyond this, the large sample size in this study allowed us to show that vervet foraging decisions were much more complex than this simple dichotomy. Adult males, who had little risk of being displaced by a dominant competitor, tended to take the path that minimized travel distance unless they were foraging in direct competition. Given that they rarely had dominant audience members, it is likely that adult males were sensitive to the risk that a subordinate group member would steal the banana before they were able to displace them, or they wanted to avoid the conflict that might erupt from doing so. Adult females and subadults, whose lower rank meant they experienced high levels of contest competition at the experiment, appeared to assess the likelihood they would lose the preferred-food reward to a dominant competitor if they stopped to feed at low-value corn platforms first. If they were still slow at retrieving the banana from the food box (i.e., high handling-time, low skill), or if a higher-ranking group member was relatively close by (26–50 m away) so as to have a short travel time, adult females and subadults were more likely to rush for the preferred-food platform at the onset of the trial. However, if dominant audience member(s) had a longer travel time because they were 51–75 m away, adult females and subadults were more likely to take the time to eat one platform of corn on their way to their preferred food reward.

Handling times were highly variable (range: 1–69 s) and experience with the box improved most vervet's skill in retrieving the banana from the box (i.e., decreased handling time) (Arseneau-Robar, unpublished data). For low-ranking individuals, handling skill impacted route choice decisions. Since food profitability improves considerably as handling time decreases (Pyke, 1984; Stephens and Krebs, 1986) and aggression levels decrease (Sirot, 2000; Johnson et al., 2001), experienced and proficient vervets could put in less effort, receive less aggression, and improve their energy gain. This allowed low-ranked individuals to forage more efficiently by saving on distance costs, and get all of the resources in the array when dominants were far enough away that their travel time to the array was great. Surprisingly, having a dominant audience member within 25 m did not affect the routing decisions of low-ranking monkeys as much as having dominants further away. This pattern was likely observed because when two individuals were within 25 m of the platforms at the onset of the trial, the lower-ranking individual typically waited for the dominant to take priority-of-access to the platforms of their choice. As a result, subordinate individuals tended to be the competitor rather than the focal, meaning we had a small sample size of trials in which the focal had a dominant audience member within 25 m. The propensity of subordinates to wait and see how many platforms they would be tolerated at highlights the need for future work to examine the contexts in which dominants tolerate subordinates at the array. Such investigations will improve our understanding of how both dominant and subordinate individuals make flexible decisions when foraging in competition.

We predicted that proficiency and skill in handling time would lead to more efficient foraging routes, regardless of dominance rank. Dominant animals, however, did not seem to make route choice decisions based on their skill level. Relative to subordinates, dominants were more likely to minimize travel distance, probably because they were not under pressure from audience members. Despite this, we did find that the alpha male was more likely to employ the intermediate strategy of getting one corn en route to the preferred-food platform, as opposed to minimizing travel distance. This pattern may have arose because he could monopolize the experiment until satiated. When nearing satiation, decision-makers sometimes decreased their consumption of the less-preferred corn, only eating the platform that was directly on their travel path to the more-preferred banana. If they continued to run trials, they could eventually only visit the platform with the banana, leaving all the corn platforms for a subordinate group member. This is similar to dominant male chacma baboons, who have been previously shown to prefer high-handling time patches because of their ability to monopolize them and kleptoparasitize others if they are already present (Marshall et al., 2012). Alternatively, the alpha male may have displayed high levels of tolerance toward competitors, allowing them to consume a larger proportion of the food rewards provided (ESM 6).

Animal foraging behavior is often altered in social contexts where an audience is present (Giraldeau and Caraco, 2000) and the risk of kleptoparastism increases (e.g., Hockey and Steele, 1990; Heinrich and Pepper, 1998; Jones et al., 2018). The presence of a dominance hierarchy usually means that the consequences of contest competition for food are experienced much more intensely by low-ranking animals that may need to adopt alternate strategies to gain food (e.g., Adams et al., 1998; Hollis et al., 2004a,b). In previous research, the effects of dominance rank and an audience in altering foraging behavior have been most clearly demonstrated in food caching species (Clarke and Kramer, 1994; Lahti and Rytkönen, 1996; Lahti et al., 1998; Dally et al., 2005; Samson and Manser, 2016). For example, in Cape ground squirrels (*Xerus inauris*), only low-ranked individuals, who were likely to lose food to dominants, avoided caching food when audience members were attentive to them (Samson and Manser, 2016). In primates, species dominance style has been linked to the strategies used by subordinates to retrieve food around dominants, with more despotic macaque species showing sneakier tactics by subordinates than more tolerant macaques (Gomez-Melara et al., 2021).

In the case of our vervet subjects, we observed the development of complex strategizing and decision-making by low-ranking individuals. Because male vervet monkeys are approximately 1.5 times larger than females and have bigger canines, adult males tend to be dominant to other age-sex classes [for exceptions see Young et al. (2017), Hemelrijk et al. (2020), and Li et al. (2021)]. Since the experimental array was set up in an area with good visibility for at least 100 m in each direction, low-ranking individuals were able to accurately assess competitor pressure, which allowed them to plan ahead (i.e., Mugan and MacIver, 2020) and make future-oriented predictions about competitor movements. Indeed, low-ranking monkeys in our study made quick routing decisions that were predicated on their own handling skill, the composition of the audience, and how far away certain individuals were. To do this, they needed to identify others and their relative rank and then assess whether they had enough time and were skilled enough to get corn and extricate the banana before dominants, given their distance and potential speed of travel, were able to arrive at the array. This shows complex, multifactor decisions that consider a great deal of contextual information. Interesting questions for future studies would be whether low-ranking monkeys further modulate their decisions according to features of their audience members other than their relative rank. For instance, do decision-makers consider how fast different group members can run or whether that audience member previously approached the experiment to be a competitor? Do they monitor audience members to see if they are attending to the experimental site, or not, as a means of assessing the likelihood the audience member will approach?

Simple heuristic rules can be used to decide on an action based on whether or not a dominant is in the audience (e.g., *Cercocebus torquatus atys*, Range and Noë, 2005); however, choosing an action based on the relative distance of dominants and their likely speed may require flexible decision-making abilities (Janmaat et al., 2014), and greater cognitive effort. Relational physical, spatial, and temporal reasoning are needed to track a particular individual and infer where and how fast they will move. These types of cognitive skills are likely ancient though, given their importance in prey tracking, as well as the long history of gregariousness in many animal lineages. Yoo et al. (2020) used joystick-trained rhesus macaques (*Macaca mulatta*) to do a pursuit task where "prey" were programed to follow intelligent escape algorithms. They found that the monkeys used the position, velocity, and acceleration (i.e., the three Newtonian variables) of prey to make accurate predictions about their future locations. In both this task and an evasion task (Yoo et al., 2021), neurons in the dorsal anterior cingulate cortex (dACC), which receives information from reward and navigational regions of the brain and transmits information to motor brain regions, were identified as active. Thus, the dACC may play an important role in tracking the elemental physical variables of position, velocity, and acceleration for the self, the prey, and the predator. It is possible that the same neural processes are involved when tracking the movements of competing group members to make predictions about their future positions relative to one's own.

For decades, researchers have debated whether social or ecological selective pressures have driven the evolution of advanced cognition (Jolly, 1966; Parker and Gibson, 1977; Milton, 1981; Gibson, 1986; Byrne and Whiten, 1988; Byrne, 1988; Tomasello and Call, 1997; Dunbar, 1998; Sol et al., 2005; de Waal, 2007; Dunbar and Shultz, 2007; Burkart et al., 2009; Sol, 2009). However, it is increasingly argued that these social and ecological hypotheses are not mutually exclusive (Cunningham and Janson, 2007; Janson and Byrne, 2007), and that each of these selective pressures may have had domain-specific effects on the cognitive systems a species evolves (Rosati, 2017). Our study highlights the important role that social context plays in shaping foraging decisions, and the complexity that this dimension adds to the decision-making process. To successfully outcompete their group members, decision-makers need to attend to, process and respond to a multitude of ecological and social stimuli simultaneously, and flexibly adapt their behavior to optimize resource acquisition while also mitigating the loss of resources to competitors. Our findings suggest that in gregarious species, where foraging often takes place in dynamic social contexts, decision-makers likely utilize numerous social and ecological cognitive processes simultaneously. How social and ecological cognitive processes integrate together to determine the capacity for flexible decision-making behavior in gregarious species, is an exciting avenue of future research in comparative cognition.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The methods were approved by the Uganda Wildlife Authority, the Uganda National Council for Science and Technology, and the University of Toronto Animal Care Committee.

AUTHOR CONTRIBUTIONS

TJA-R and JT designed the study, analyzed the data, and wrote the manuscript. JT and PS funded the study. TJA-R collected the data. KA, EV, and TJA-R coded the data from video. All authors helped to edit the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.775288/full#supplementary-material

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Individual Variation in Response to Novel Food in Captive Capuchin Monkeys (*Sapajus* spp.)

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How animals respond to novelty may have important outcomes in terms of fitness. On the one hand, aversion to novel stimuli may reduce the risks of consuming potentially toxic food or encountering predators. On the other hand, the propensity to approach novel stimuli may allow individuals to explore novel food sources and more flexibly adapt to novel challenges. Different species and individuals may find different ways to balance the costs and benefits that novelty posits. To date, however, little is known on how response to novel food varies across individuals of the same species depending on their previous experience with novelty, risk attitude and presence of higher-ranking conspecifics. In this study, we assessed individual variation in response to novel food by testing captive capuchin monkeys (*Sapajus* spp.) in an unconstrained social context, where all individuals in a group were able to access the testing area on a voluntary basis. We provided familiar and novel food to 23 study subjects belonging to four social groups differing in (i) previous experience with novel food, (ii) risk attitude (as assessed by a previous risky decision-making task), and (iii) dominance rank. We predicted that, as individuals may generalize their previous experience to novel contexts, those with more previous experience with novel food would be less neophobic than those with less experience. Moreover, if neophobia is a facet of the individual's risk attitude, we predicted that more risk-prone individuals would be less neophobic than less risk-prone ones. Finally, individuals might flexibly modify their food choices according to the presence of conspecifics; in this respect, we predicted that, in response to monopolization of preferred resources by higher-ranking individuals, lower-ranking individuals would prefer familiar over novel food in the absence of higher-ranking individuals, but would modify their preference in favor of novel food in the presence of higher-ranking individuals. None of these predictions were supported by our results. We observed, however, that neophobia, measured as the latency to retrieve a food item, was more pronounced in lower-ranking than higher-ranking individuals, and that males showed a generally stronger bias than females toward a quicker retrieval of familiar food.

Keywords: novel food, neophobia, primates, capuchin monkeys, individual variation, previous experience, risk attitude, social context

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INTRODUCTION

Animals face a variety of stimuli during their everyday life, some of which entail a degree of novelty because they have never been previously experienced. On the one hand, aversion to novel stimuli may be adaptive to, for instance, reduce the risks of consuming novel and potentially toxic food (Greenberg and Mettke-Hofmann, 2001; Ferrari et al., 2015). On the other hand, individuals attracted by novel stimuli may be more explorative and innovative, and thus more likely to encounter novel resources, solve novel problems and flexibly adapt to novel challenges (birds: Greenberg, 2003; Overington et al., 2011; Sol et al., 2011; Griffin and Diquelou, 2015; primates: Webster and Lefebvre, 2001; Day et al., 2003; Amici et al., 2020a). Therefore, how animals react to novelty may have important outcomes in terms of fitness (Crane et al., 2020), and different species and individuals may find different ways to balance the costs and benefits of novelty, depending on the socio-ecological challenges they face (Greenberg and Mettke-Hofmann, 2001; Mettke-Hofmann et al., 2002; Forss et al., 2017; for a review see Mettke-Hofmann, 2014; Miller et al., 2022).

Animals may avoid novel stimuli (i.e., showing neophobia), they may be attracted by novelty (i.e., showing neophilia) or they may neutrally respond to novel stimuli. Although neophobia and neophilia may be considered two extremes of the same continuum, they are best conceptualized as independent responses (Russell, 1973), resulting from the dynamic balance of fear and curiosity (Hughes, 2007). Here, we will define neophobia as the avoidance behavior that arises when the novel stimulus generates a fear response (Greggor et al., 2015). Neophobia can be context-specific (e.g., gustatory, predator, social, object or spatial neophobia; Crane et al., 2020), and can strongly vary depending on the specific stimuli experienced (Greggor et al., 2015). Different methods can be used to assess neophobia, including the time individuals spend in proximity to the novel stimulus, the latency to approach or retrieve the novel stimulus or the number of novel food items consumed. Therefore, response to novelty may strongly vary within individuals, depending on the context, the stimuli and methods employed to assess this behavior.

To date, the vast majority of studies have compared neophobia across different species, to investigate the socio-ecological conditions that may be linked to the emergence of higher neophobia in certain species (e.g., birds: Mettke-Hofmann et al., 2002; ungulates: Schaffer et al., 2021; primates: Addessi et al., 2004; Addessi and Visalberghi, 2006; Bergman and Kitchen, 2009; Forss et al., 2019; Amici et al., 2020b). Other studies, however, have focused on individual variation in neophobia (e.g., birds: Mettke-Hofmann et al., 2005; Fox and Millam, 2007; Ensminger and Westneat, 2012; ungulates: Schaffer et al., 2021; primates: Amici et al., 2020b). Neophobia, for instance, may vary across conspecifics depending on their age, sex or rank. In birds, Biondi et al. (2010) have shown that adults are more neophobic than juveniles toward novel objects. A similar effect has been found in primates tested with novel food (wild capuchin monkeys (*Cebus apella*): Visalberghi et al., 2003a; captive chimpanzees (*Pan troglodytes*): Addessi and Visalberghi, 2006), although other studies have found no significant relation between age and neophobia (wild capuchin monkeys (*Cebus libidinosus*): Sabbatini et al., 2007; captive great apes (*Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*, *Pongo abelii*): Gustafsson et al., 2014) or, in contrast, the opposite pattern was observed (captive marmosets (*Callithrix jacchus*): Yamamoto and de Araújo Lopes, 2004; Voelkl et al., 2006). Moreover, sex may predict differences in neophobia: some authors argued that males should be less neophobic than females, because competition through sexual selection is more intense for males, who would thus need higher behavioral flexibility (Schuett et al., 2010; Crane et al., 2020). However, since in mammals males are usually higher-ranking than females, sex-rank effects might be confounded (Crane et al., 2020). Indeed, studies on primates have found contrasting results: in captive capuchin monkeys, for instance, sex and rank were not found to affect preference toward novel food (Visalberghi et al., 2003b) but, in a study on wild capuchin monkeys, females showed a less neophobic response toward novel objects than males, while rank had no significant effect (Visalberghi et al., 2003a).

In terms of sociality, different factors may explain individual variation in response to novelty. In social species, for example, higher-ranking individuals usually have priority of access to resources (Ellis, 1995; Altmann, 1998; Hohmann et al., 2006). Moreover, primates who are more integrated in their social group may also have better access to resources (Amici et al., 2020b; Dell'Anna et al., 2020). Therefore, higher-ranking or more socially-integrated individuals may receive a lower potential payoff from novel stimuli, and may be more neophobic than lower-ranking or less socially-integrated individuals (Hegner, 1985; Greenberg-Cohen et al., 1994; Lahti, 1998; Wolf et al., 2007; An et al., 2011). Furthermore, in some species the presence of a conspecific may facilitate the acceptance of novel food or objects (birds: Coleman and Mellgren, 1994; Huber et al., 2001; rodents: Forkman, 1991; canids: Moretti et al., 2015; primates: Visalberghi and Addessi, 2000; Voelkl et al., 2006; Hardus et al., 2015). The latter findings may result from very different processes. On the one hand, social facilitation may reduce neophobia (Addessi and Visalberghi, 2001). On the other hand, especially in a foraging context, novel resources may be accepted as a means to reduce competition (Amici et al., 2020b).

Beyond age, sex and sociality, other factors like previous experience and risk attitude might also explain individual variation in response to novelty, although these factors have been usually overlooked in previous studies. Differences in neophobia may partly result from the complex interactions that individuals have with the environment during their life (Greenberg, 2003; Biondi et al., 2010). For instance, response to novelty may depend on how much the novel stimulus differs from other familiar stimuli, and thus on how easily familiar features can be generalized to novel stimuli. Generalizations to novel stimuli have been well documented both in the context of foraging (e.g., Greenberg, 1990; Greenberg and Mettke-Hofmann, 2001) and in the context of predation (e.g., Brown et al., 2013). In lambs, for example, early life experiences with novel food reduces neophobia when individuals are exposed to other kinds of novel food (Catanese et al., 2012). In whitetail damselfish (*Pomacentrus chrysurus*), previous experiences with predators predict a decrease in neophobia toward predators

(Crane and Ferrari, 2017), with higher neophobia (and higher survival rate) in individuals with no previous experiences of escaping from predators (Ferrari et al., 2015). However, the link between previous experiences and neophobia may be context-specific, as shown by a recent study finding that early predator experience did not affect the latency of the daffodil cichlid (*Neolamprologus pulcher*) to feed near a novel object (Bannier et al., 2017).

Neophobia may also reflect how animals generally assess uncertainty. Animals face uncertainty because they do not always know the outcome of their decisions. Studies with non-human primates have assessed how animals react to uncertainty by testing their risk attitude (Heilbronner et al., 2008; MacLean et al., 2012; Rosati and Hare, 2012; De Petrillo et al., 2015). In these tasks, individuals are usually presented with a series of choices between two options, one yielding a reward that is constant in amount (safe option) and one yielding a reward that varies probabilistically around the mean (risky option), with the two options leading on average to the same payoff. Individuals with a preference for the risky option are considered risk-prone, whereas those with a preference for the safe option are considered risk-averse (Kacelnik and Bateson, 1996). While these studies consider risk as the failure to receive a reward, animals in their own environment also face the risk of losing valuable resources or being physically injured (Paglieri et al., 2014). Neophobic behaviors may represent an individual's reaction to uncertainty due to a lack of information associated with a novel stimulus (Crane et al., 2020). Risk-prone individuals may focus on the potentially valuable payoff that novelty offers rather than on its risky outcome. Thus, it should be possible that risk proneness and neophobia are two related traits and that the individual attitude to face risk shapes the response to novelty (Greenberg, 2003).

In the present study, we investigated inter-individual variation in neophobia toward novel food and, in particular, the role of previous experience and risk attitude on how individuals respond to novelty in a social setting. We did so in an unconstrained social setting, where all individuals in a group could freely participate in the experiment on a voluntary basis, thus mimicking the social context in which individuals usually interact with novel stimuli in their daily life, and allowing more meaningful comparisons with data collected in the wild. We used capuchin monkeys as a model species, assessing their relative preference for novel and familiar food and their latency to retrieve it under two different conditions. Capuchin monkeys have been largely studied both in the wild and in captivity for their complex foraging strategies (e.g., tool use, Visalberghi and Limongelli, 1994; Fujita et al., 2011; Falótico and Ottoni, 2016; processing of toxic foods, Sirianni and Visalberghi, 2013) and their neophobic response to novel food and objects (e.g., Addessi et al., 2004; Addessi and Visalberghi, 2006). We expected inter-individual differences in how capuchin monkeys react to novel food. In particular, we predicted that more experienced individuals (i.e., having been more frequently exposed to novel food in previous studies) would be less neophobic than less experienced ones. Moreover, we predicted that more risk-prone individuals (i.e., those that preferred a risky option over a safe one when confronted with two options yielding on average the same payoff; De Petrillo et al., 2015) would be less neophobic than less risk-prone ones. Finally, we predicted that the presence of higher-ranking individuals would affect the choice of lower-ranking ones, so that the latter would prefer familiar food to novel food in the absence of higher-ranking individuals, but would reverse their preference in the presence of higher-ranking individuals. We tested for our predictions while controlling for age, sex and rank, which were found to be significant predictors of neophobia in previous studies. We did not explicitly control for reproductive status and past reproductive experience because the last pregnancies in the colony occurred 10 years ago and because reproductive experience is correlated to sex and age, already included in the analysis.

MATERIALS AND METHODS

Ethics

This study complied with protocols approved by the Italian Health Ministry (DM 633/2020-PR to the last author). All procedures were performed in full accordance with the ethics requirements of the Directive 2010/63/EU on the protection of animals used for scientific purposes and conformed to the "Guidelines for the treatment of animals in behavioral research and teaching" (Bee et al., 2020).

Subjects

The study involved 23 subjects belonging to four social groups (Group 1 = 5 subjects; Group 2 = 5 subjects; Group 3 = 4 subjects; Group 4 = 9 subjects; **Table 1**), hosted at the Primate Center of the Unit of Cognitive Primatology, Institute of Cognitive Science and Technologies, National Research Council of Italy, Rome, Italy. In the colony we tested some changes in group composition occurred in the past years. However, from 2004 the composition of our groups was rather stable. Seventeen out of the 23 subjects had previously participated in studies in which they were presented with novel food (**Table 1**). Eight out of the 23 subjects had previously participated in a risky decision-making task (**Table 1**). All groups were housed in enclosures with indoor and outdoor areas. The indoor area measured 25.4 m^3 for all groups, and was divided in two sections; the outdoor area measured 53.2–374.0 m^3 depending on the study group. All enclosures were furnished with wooden perches, tree trunks and branches. Testing occurred in the morning, between 09:30 and 13:30 h, before the main meal, and water was available *ad libitum*. Individuals participated on a voluntary basis. Data were collected in November and December 2020.

Experience, Risk Attitude and Social Context

Subjects participated to a variable extent in previous experiments testing their reaction to novel food (**Supplementary Table 1**). Previous experiments using novel food were carried out for about 10 years since 1992 and used both fresh fruits and vegetables

TABLE 1 | Individual characteristics of the study subjects, including their name, group, age (in years), sex, rank (with 1 referring to the highest-ranking individual in each group), experience with novel food (as the number of experiments on neophobia in which each subject had participated before being tested), risk attitude (as the mean proportion of trials in which the subject had chosen the risky over the safe option in a decision-making task; De Petrillo et al., 2015) and number of total sessions of conditions A and B in which each subject participated.

Name	Group	Age (years)	Sex	Rank	Experience with novel food	Risk attitude	Number of participated sessions
Sandokan	1	20	M	1	0	0.97	21
Vispo	1	20	M	2	1	–	21
Pepe	1	33	M	3	8	–	5
Virginia	1	21	F	4	2	–	0
Roberta	1	34	F	5	8	0.81	21
Gal	2	30	M	1	8	0.45	20
Totò	2	10	M	2	0	–	20
Rame	2	33	F	3	8	–	20
Paprika	2	31	F	4	7	0.56	11
Brahms	2	38	F	5	3	–	1
Robot	3	25	M	1	5	0.95	21
Patè	3	29	M	2	3	–	17
Saroma	3	19	F	3	0	0.98	11
Robinia	3	27	F	4	4	0.41	3
Robin Hood	4	23	M	1	4	0.95	20
Peonia	4	26	F	2	0	–	20
Penelope	4	21	F	3	2	–	20
Cognac	4	33	M	4	8	–	20
Ulisse	4	10	M	5	0	–	14
Quincy	4	17	F	6	0	–	20
Pacajà	4	23	F	7	2	–	8
Rucola	4	20	F	8	1	–	6
Robiola	4	22	F	9	3	–	2

(e.g., pineapple, kiwi, tomato, celery, broccoli) and processed food (e.g., mashed canned "Spagna" beans, colored blue; mashed boiled skinned lentils, colored red; mashed boiled aubergine colored green; mashed canned "borlotti" beans, colored violet; semolina cooked with water and sugar). As a proxy of experience with novel or unfamiliar food, we used the number of such experiments in which each subject had participated before being tested in the present study. Some subjects ($N = 8$; **Table 1**) had also participated in a decision-making task requiring them to choose between a safe option (i.e., yielding a constant reward) and a risky option (i.e., yielding a reward that probabilistically varied around the mean; De Petrillo et al., 2015). We used the mean proportion of trials in which each subject had chosen the risky option as a proxy of his/her risk attitude. Although this experiment was performed a few years before the current study, relative risk attitude among subjects seems to be a stable trait in humans (Straznicka, 2012; Josef et al., 2016) and, while detailed information for capuchin monkeys is still lacking, new data collected in 2019 on our study subjects (which we did not employ in the present study as they have not been published yet) showed no significant difference from those collected in 2014 by De Petrillo et al. (2015). Since our study subjects were tested in a social context, we also tested whether reaction to novelty by lower-ranking subjects was affected by the presence of higher-ranking individuals. To evaluate this effect, every time we observed a monkey retrieving a food item, we measured the difference between the rank of the subject retrieving the food item and the rank of the highest-ranking individual present in the testing area at the time of retrieval. The dominance hierarchy was obtained from the observation of the direction of dyadic unidirectional agonistic interactions among group members. Since capuchins' societies are characterized by a high degree of tolerance, aggressions are very rare and rank determination within capuchin groups held at ISTC-CNR Primate Center is updated continuously based on opportunistic observations. Moreover, before the start of the experiments, we used the "peanut test" to resolve ambiguous cases (i.e., where the hierarchical position of two individuals was not well defined). The test consisted in placing a peanut in the middle of a cage, equidistant from the two individuals and observing which subject retrieved it, and it was administered four times for each of the three "ambiguous" dyads. In all cases, the same subject retrieved all of the peanuts.

Procedure

We exposed subjects to novel and familiar food in a social setting, which better mirrors the natural context in which captive and wild individuals usually interact with novel stimuli. During the sessions, subjects could freely move between the indoor and outdoor areas of their enclosure. Food items (banana slices) were distributed on the floor of two adjacent sections of the indoor area (hereafter, "testing areas"), connected through sliding doors to the outdoor area of the enclosure (**Supplementary Figure 1**). We distributed food items on the testing area floor so that they were as evenly distributed as possible while ensuring visibility from the point of view of recording cameras (section "Coding"). In each testing area, we distributed a number of food items which was proportional to the number of individuals in the group (i.e., four food items per individual, with the only exception of two groups who received a lower number of food items in the first session, i.e., two food items per individual). Half of the food items were familiar banana slices, and the other half were "novel" banana slices, which had been dyed with odorless and tasteless food coloring (Lo Conte, decorì). Since novelty has been shown to increase with stimulus complexity (Greggor et al., 2015), we also added a novel texture to the "novel" banana slices, covering those with seeds that subjects had never eaten before. We administered two conditions, which were identical except for the kind of novel stimuli used: blue banana slices with sesame seeds (condition A), and red banana slices with poppy seeds (condition B). The order of the two conditions was counterbalanced across the study groups to control for order effects (i.e., Groups 1 and 4 received condition A before condition B, whereas the order was reversed for Groups 2 and 3). We administered 10 sessions (with the exception of two groups who received a lower number of food items in the first session and to which we administered 11 sessions) for each study group and condition (total number of sessions: 82). To maintain motivation high, we only administered one session per day.

Coding

We videotaped each session, and also verbally announced on video the identity of every individual entering the testing areas. Each session started when the sliding doors connecting the indoor and outdoor areas opened so that individuals were able to enter into the testing areas, and it ended when all the banana slices had been eaten (mean session duration: 216 s; min-max 81–511 s). By using the software BORIS (Friard and Gamba, 2016), we later coded from the videoclips, for each episode of food retrieval (i.e., an observed event of one monkey retrieving one banana slice, hereafter, "retrieval episode"), the identity of the individual retrieving the food, and the type of food retrieved (i.e., familiar or novel). Subjects ate almost all of the food items they retrieved. In only 39 instances out of a total of 1,936 observed episodes of food retrieval, the food item was dropped. Moreover, for each session and individual, we coded the latency to retrieve familiar food and the latency to retrieve novel food. Latency to retrieve familiar food was defined as the time elapsed from the first entrance of a subject in one of the two testing areas and the first retrieval of a familiar food item in the session. Similarly, latency to retrieve novel food was the length of the time interval between the first entrance of the subject and the first retrieval of a novel food item. Videos were independently coded by two observers (MV and GSg). Inter-observer reliability was assessed on 20% of recordings for familiar food retrieval (ICC = 0.996), novel food retrieval (ICC = 0.998), latency to retrieve familiar food (ICC = 0.997), and latency to retrieve novel food (ICC = 0.997).

Statistical Analyses

We performed all statistical analyses and plotting using R v. 4.1.0 (R Core Team, 2021). We used the glmmTMB package (version 1.1.2.3; Brooks et al., 2017) to fit (Generalized) Linear Mixed Models (GLMM, Baayen et al., 2008).

In our experimental design, an equal number of familiar and novel food items was presented to the monkeys at the beginning of each session (section "Procedure"). However, as the session proceeded and food items were consumed by the monkeys, the absolute number of available food items decreased, and the relative number of familiar and novel items changed erratically. We operationally defined preference for retrieving familiar over novel food as the marginal probability to retrieve a familiar food item estimated by a binomial model, where the response was whether each retrieved food item was familiar (1) or novel (0) and which included a term to account for the relative availability of familiar over novel food items (i.e., the proportion of familiar to novel food available when each food item was retrieved).

To test if each individual's *preference* for retrieving familiar or novel food (i.e., the probability to retrieve one type of food or the other, accounting for their availability) depended on his/her experience and the presence of higher-ranking individuals, we fitted a GLMM (M1) with binomial error structure and *logit* link function, where the binary dependent variable was whether, for each retrieval episode, the food retrieved was familiar or novel (*food type*). As test predictors, we entered the subject's experience (*experience*, i.e., number of previous experiments involving the presentation of novel foods in which she/he had participated), the difference between the subject's rank and the rank of the highest-ranking individual in the testing area at the moment of food retrieval (*rank difference*), the cumulative number of food items retrieved by the subject in the course of the experiment for each condition before the current retrieval episode (*n. retrieved items*, which allowed to control for the decreasing novelty of the "novel" food in the course of the experiment), the subject's *rank*, and the 2-way interactions of *experience*, *rank difference* and *rank* with *n. retrieved items*. The three interactions model the predictions that the effect of *experience*, *rank difference* and *rank* may change as the novel items become increasingly familiar (in particular, the effect of *rank difference* on food preference may change as the higher-ranking individuals change their preference across sessions, which affects their potential monopolization of preferred food). We note that our definition of the term controlling for decreasing novelty of the "novel" food as the number of retrieved food items formally implies the assumption that monkeys only acquire experience when they do retrieve food items, rather than by just standing by while the experimental sessions unfold. While this assumption appears reasonable to us, we appreciate that, at least when they enter the cages, monkeys may acquire some familiarity with the novel food by just standing by and looking. However, we remark that, by including a term for the interaction of *rank* and *n. retrieved items* our analysis is in fact flexible enough to adjust to either of these assumptions or to a combination of them (of course, with potential changes in the interpretation given to significant terms for *rank*, *n. retrieved items* and their interaction). As controls, we included the individuals' *age*, *sex* and *group*, the *condition* (A or B), the number of food items which was proportional to the number of individuals in the group (*food per subject*) and, importantly, the proportion of familiar vs. novel food available when food was retrieved (*proportion familiar*, which ensured that our analysis actually modeled retrieval *preference*, rather than choices dictated by availability). Individual identity (*subject*) was included as a random intercept. As a binomial model only allows for probabilities (in this case representing retrieval preferences) to "plateau" at 0 or 1, we aimed at avoiding episodes of food retrieval happening after complete disappearance of "novelty" effect (i.e., when the plateau had been reached) by only including the first 10 retrieval episodes for each individual, condition and food type. We fitted model M1 on 383 observations from 22 individuals.

In a second model (M2), we further tested whether individuals preferentially retrieved familiar or novel food depending on their risk attitude, as measured in De Petrillo et al. (2015). As we did not have risk-attitude data for all individuals, we only used a subset of 8 individuals. Model M2 was similar to M1 and considered the same test predictors as M1, plus the individual risk-attitude score (*risk attitude*, see section "Materials and Methods") and the 2-way interaction between *risk attitude* and *n. retrieved items*. In order to overcome collinearity, we had to remove *group* (only one subject in group 4), *age* (collinear with *experience*) and *sex* (collinear with *rank*) from the controls. In M2, therefore, we included, as controls, *proportion familiar*, *food per subject* and *condition*, as well as *subject*, modeled as a random intercept. Again, only the first 10 retrieval episodes for each individual, condition and food type were considered (total number of observations = 148).

In a third model, we assessed which factors predicted participation in the experiment by fitting a GLMM (M3) with binomial error structure and *logit* link, where the binary response variable was whether the subject entered the testing area at least once during each session (*participation*). As test predictors, we included the 2-way interaction of subject's *experience* with *session number* (the cumulative number of sessions for each group and condition), and the 2-way interaction of subject's *rank* with *session number* (for a rationale, see M1). As, in this model, each observation represented a combination of one individual and one whole session, in which all members of its group could, potentially, participate, it would not make sense to consider rank difference as a predictor. As controls, we included individuals' *age* and *sex*, and *condition*. *Group* was not included as a control factor in this model because we detected high collinearity of *group* and *rank* (VIF = 12.6 and 11.5, respectively). Individual identity (*subject*) was included as a random intercept. We fitted model M3 on 469 observations of 23 individuals.

To test whether *experience* and *rank* of individuals affected their latency to retrieve familiar or novel food, we fitted a LMM (M4) where the (log-transformed) *latency* time was the response variable (see section "Materials and Methods" for latency definition). As test predictors, we included the 3-way interaction of subject's *experience* with *session number* and *food type* (familiar or novel), and the 3-way interaction of subject's *rank* with *session number* and *food type*, plus all the 2-way interactions and main effects included in them. We did not include rank difference in this model because observations referred to time intervals that could extend up to more than 2 min (max latency time was 139 s), so that it was not possible to determine a single value for the rank difference which would be valid for the whole observation. The rationale for this model structure was that the difference in latency times between novel and familiar food is expected to decrease according to the subject's experience and rank, but this effect may be weaker in higher-ranking individuals, and might decrease through sessions. As controls, we included individuals' *age*, *sex*, and *group*, the *condition*, plus the interaction of *sex* and *food type* (modeling sex differences in neophobia). We included random intercepts for *subject* and *session identity*, as more than one data point was entered for each individual in each session. As not all individuals participated in all sessions, latency times were not available for all individuals in all sessions (number of observations = 549, number of subjects = 22).

Last, we fitted a model similar to M4 which also included *risk attitude* among the predictors and a term for the 3-way interaction of *risk attitude* with *session number* and *food type* (M5). We fitted M5 on a subset of 219 observations from the 8 individuals for which risk-attitude scores were available. As for M2, we had to remove *group*, *age* and *sex* from the controls so to avoid collinearity issues. Moreover, we could not include a random intercept for *session identity* as this would have resulted in over parameterization and lack of convergence.

In all models, we z-transformed all quantitative predictors. We compared full models (containing test predictors, controls, and random factors) to null models (only containing controls and random factors) by Likelihood Ratio Test, using the R function "ANOVA." We obtained the p-values for each term using the R function "drop1" (Dobson and Barnett, 2018). If full-null model comparison was not significant ($\alpha = 0.05$), we only computed p-values for control terms. If an interaction was not significant, we re-run the model after downgrading it. We used the DHARMa R package v. 0.4.4 (Hartig, 2021) to assess the distribution of residuals and check for violation assumptions. Collinearity among predictors was measured by Variance Inflation Factors (VIF) estimated using the function "check_collinearity" (R package performance, Lüdecke et al., 2021). We considered the thresholds suggested by the performance package. VIF < 5: low collinearity; 5–10: moderate collinearity; > 10: high collinearity. We found no convergence or over/under-dispersion issues in the models presented. We checked for the robustness of model results to influential cases by re-fitting each of the final models after removing observations from one subject at a time. Except where noted, we did not detect any important effect of influential cases.

As the four social groups involved in our study comprise different numbers of subjects (section "Experience, Risk Attitude and Social Context," **Table 1**), we also considered employing a standardized measure of rank (and rank differences), so as to eliminate correlation between absolute rank and belonging to a particular group. We refitted all of our models after standardizing rank and rank difference within each group to a [0,1] interval. This procedure allowed to eliminate the collinearity between group and rank in model M3 allowing to keep group among the control terms in M3. However, the results of none of the models changed appreciably.

Data tables and the complete R script including all steps of data analysis are available as **Supplementary Data Sheet 1**.

RESULTS

In M1 and M2, we assessed which factors predicted individual preferences to retrieve familiar over novel food. For M1, the full-null comparison was not significant ($\chi^2 = 8.85$ $df = 7$, $p = 0.264$). Among the controls, besides the trivial effect of the proportion of familiar food items available (*proportion familiar*), only *condition* was significant ($p < 0.001$; **Table 2**), with monkeys retrieving novel items more likely in condition A (i.e., blue banana slices with sesame poppy seeds) than in condition B (i.e., red banana slices with poppy seeds), indicating that the different treatment of "novel" food items significantly affected the reaction of monkeys. In particular, by taking the estimated values from model M1 for the intercept, proportion of familiar items available and condition (and keeping all other, non-significant, coefficients at their sample mean), the overall probability for a monkey to retrieve the novel item when both familiar and novel items were equally available, throughout the first 10 retrieval episodes for each subject and condition, could be calculated at 0.63 and 0.37, respectively, for condition A and B (**Figure 1**), indicating that, as far as the *preference* for novel over familiar food is concerned,

TABLE 2 | For models M1 and M2, test predictors and controls (in italics) included in the final model, estimates, standard errors (SE), *z*-values (*z*), confidence intervals (CIs), likelihood ratio test's χ^2 (LRT), degrees of freedom (*df*) and *p*-values.

M1: neophobia as preference for familiar over novel food (binomial)

Term	Estimate	SE	Z	2.5–97.5% CI	LRT	df	p
Intercept	−1.70	1.30	−1.31	−4.26 to 0.85	–	–	–
Experience	0.59	0.45	1.31	−0.29 to 1.47	1.78	1	0.182
Rank difference	0.17	0.15	1.11	−0.13 to 0.48	1.26	1	0.262
N. retrieved items	−0.02	0.12	−0.15	−0.26 to 0.22	0.02	1	0.880
Rank	0.02	0.27	0.10	−0.50 to 0.55	0.01	1	0.924
Sex (male)	−0.27	0.54	−0.50	−1.34 to 0.80	0.25	1	0.615
Age	−0.42	0.44	−0.95	−1.28 to 0.45	0.93	1	0.334
Proportion familiar	5.85	0.84	6.96	4.21 to 7.50	74.06	1	<0.001***
Condition (B)	1.05	0.28	3.79	0.51 to 1.60	15.27	1	<0.001***
Food per subject	−0.56	0.62	−0.90	−1.78 to 0.66	0.81	1	0.367
Group	–	–	–	–	3.78	3	0.286
Group (2)	−0.72	0.64	−1.12	−1.99 to 0.54	–	–	–
Group (3)	0.30	0.57	0.53	−0.82 to 1.43	–	–	–
Group (4)	−0.59	0.52	−1.12	−1.62 to 0.44	–	–	–

M2: neophobia as preference for familiar over novel food, including risk attitude (binomial)

Term	Estimate	SE	Z	2.5 to 97.5% CI	LRT	df	P
Intercept	−2.06	1.60	−1.29	−5.19 to 1.07	–	–	–
Experience	−0.67	0.33	−2.03	−1.31 to −0.02	–	–	–
Rank difference	0.08	0.30	0.25	−0.51 to 0.66	0.06	1	0.798
N. retrieved items	0.25	0.24	1.07	−0.21 to 0.72	1.38	1	0.240
Rank	0.94	0.29	3.18	0.36 to 1.51	11.47	1	<0.001***
Risk attitude	−0.23	0.29	−0.77	−0.80 to 0.35	0.61	1	0.436
Experience: n. retrieved items	−0.53	0.25	−2.16	−1.02 to −0.05	5.09	1	0.024*
Proportion familiar	9.58	1.97	4.86	5.71 to 13.44	49.10	1	<0.001***
Condition (B)	1.61	0.52	3.08	0.59 to 2.64	10.43	1	<0.001***
Food per subject	−1.38	0.80	−1.72	−2.95 to 0.19	3.12	1	0.077

*The symbol * refers to p-value < 0.05; the symbol *** refers to p-value < 0.001.*

the neophobic effect—if there was any—was generally low in our experiment, and definitely weak in condition A. In model M1, we detected moderate collinearity of *experience* and *age* (VIF = 6.7 and 6.5, respectively). We, thus, re-fitted the model after excluding age from the predictors, but the results did not change appreciably.

The full model M2 was a significantly better fit than the corresponding null model ($\chi^2 = 22.18$, $df = 9$, $p = 0.008$) to the reduced data set (including data from 8 individuals with risk-attitude score). The final M2 model revealed a significant effect of *rank*, with higher rank corresponding to a lower preference for the familiar food ($p < 0.001$, **Table 2**), and the interaction of *experience* and *n. retrieved items*, whereby more experienced individuals would decrease their preference for the familiar food with more retrieval episodes accumulated, while less experienced individuals would do the opposite ($p = 0.024$, **Table 2**). While the effect of rank may be interpreted as a higher neophobic attitude of lower-ranking subjects, the effect of the interaction is less interpretable. Moreover, that the same effect was not found to be significant in the whole dataset and was significant in an analysis of a subset of data was definitely unexpected and required deeper investigation. Model M2 differs from model M1 under three aspects: (i) *risk attitude* is a predictor in M2 but not in M1; (ii) *group*, *age* and *sex* are controls in M1 but not in M2; (iii) M1 was fitted on 383 observations from 22 subjects while M2 was fitted on a subset of 148 observations from 8 subjects. To check whether the inclusion of *risk attitude* as a predictor was responsible for the significant interaction of *experience* and *food type* in M2, we fitted a reduced version of the (final) M2 model where *risk attitude* was removed on the subset of 8 subjects (M2a). To check whether the absence of *group*, *age* and *sex* as controls was responsible for the significant interaction of *experience* and *food type* in M2, we fitted a model with the same structure as M2a to the complete data set (M2b). Both *rank* and the interaction of *experience* and *n. retrieved items* were still significant in M2a (rank: $\chi^2 = 11.76$, $df = 1$, $p < 0.001$, *experience:n. retrieved items* : $\chi^2 = 5.53$, $df = 1$, $p = 0.019$), but obviously non-significant in M2b (rank: $\chi^2 = 0.007$, $df = 1$, $p = 0.93$, *experience:n. retrieved items* : $\chi^2 = 0.203$, $df = 1$, $p = 0.65$), thus indicating that neither the inclusion of *risk attitude* nor the removal of *group*, *age* and *sex* were responsible for the differences between results of M1 and M2 and that the statistically significant effects of *rank* and the interaction of *experience* and *n. retrieved items* is an idiosyncratic feature of the smaller dataset used to fit M2.

The full model M3 significantly differed from the corresponding null model ($\chi^2 = 29.83$, $df = 5$, $p < 0.001$).

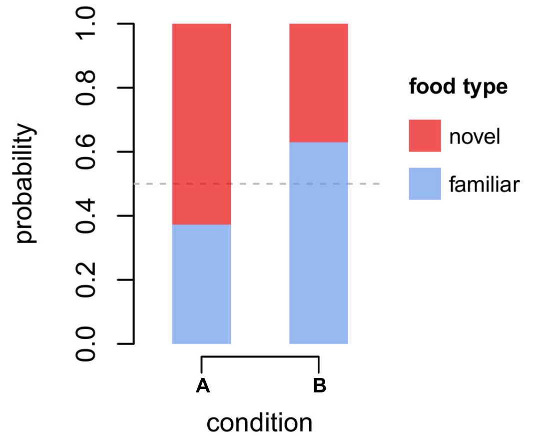

FIGURE 1 | Overall probability to retrieve the familiar (blue) or novel (red) food when both types of food were equally available in conditions A and B in the first (up to) 10 retrieval episodes for each subject and condition. Probabilities were estimated according to coefficients of model M1 (see **Table 2**), keeping all non-significant predictors at their sample mean.

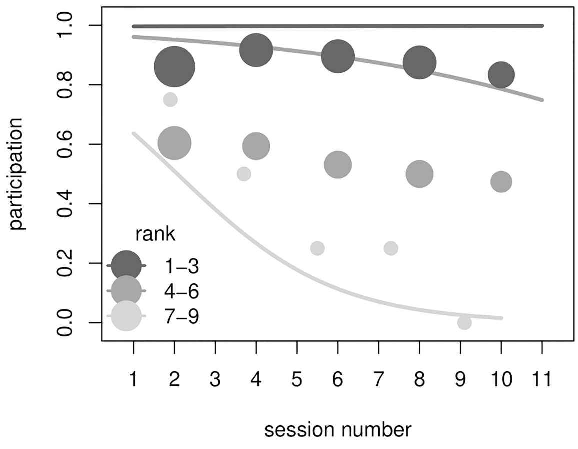

FIGURE 2 | Results from model M3. Participation in an experimental session as a function of the interaction between *rank* and *session number*. Lines show probabilities to participate in a session according to the (binned) session number and (binned) ranks as estimated by model M3 (all other predictors were kept at their sample mean). Circles show the observed frequency of participation for each rank and session bin. Shade of lines and circles represents rank (darker = higher ranking, see legend). Circles size is proportional to the number of sessions for each rank and session number bin. High-ranking individuals participated more often overall, and participation of lower-ranking individuals decreased markedly throughout the course of the experiment.

All subjects, with the exception of one individual, participated at least once in the experimental session (**Table 1**). The final model revealed a significant effect of the 2-way interaction of *rank* and *session number* ($p < 0.001$; **Table 3**). In particular, higher-ranking individuals participated more than lower-ranking ones (indeed, rank 1 individuals participated in all sessions) and participation of low-ranking individuals decreased through sessions (**Figure 2**). We signal that the p-value for the interaction between *experience* and *session number* was 0.054 (participation would be higher for more experienced individuals, which would also show more marked change between early and late sessions, not shown). Among the controls, only *condition* was significant ($p = 0.021$; **Table 3**), with monkeys participating more often in condition A.

In M4, the full-null model comparison was significant ($\chi^2 = 54.05$, $df = 10$, $p < 0.001$), with the final model revealing a significant effect of the 2-way interactions of *rank* and *food type* ($p < 0.001$; **Table 4**) and *session number* and *food type* ($p = 0.043$; **Table 4**). In particular, **Figures 3**, **4** show that latency to retrieve food was overall higher for higher-ranking than for lower-ranking individuals and that, while latency times for familiar food did not change much during the course of the experiment, latency times for novel food items decreased markedly throughout the sessions, reflecting the decreasing novelty of modified bananas. Among the controls, the interaction of *sex* and *food type* was highly significant ($p < 0.001$; **Table 4**), with females showing longer latency times than males, but only markedly so for familiar foods (**Figures 3**, **4**). Interestingly, while low-ranking individuals initially displayed longer latencies for the novel food than for the familiar food, and ended up with more similar latencies for the two types of food, the behavior of higher-ranking subjects

TABLE 3 | For model M3, test predictors and controls (in italics) included in the final model, estimates, standard errors (SE), z-values (z), confidence intervals (CIs), likelihood ratio test's χ^2 (LRT), degrees of freedom (df) and p-values.

M3: participation in a session (binomial)

Term	Estimate	SE	*Z*	2.5 to 97.5% CI	LRT	*df*	*P*
Intercept	4.00	1.84	2.17	0.39 to 7.61	–	–	–
Experience	1.64	1.71	0.96	−1.71 to 4.99	0.93	1	0.334
Session number	−0.32	0.19	−1.66	−0.69 to 0.06	–	–	–
Rank	−3.11	1.32	−1.66	−5.71 to −0.51	–	–	–
Rank: session number	−0.70	0.23	−2.98	−1.16 to −0.23	10.80	1	<0.001***
Sex (male)	−0.11	2.73	−0.04	−5.47 to 5.25	0.00	1	0.967
Age	−1.97	1.67	−1.18	−5.24 to 1.30	1.37	1	0.241
Condition (B)	−0.82	0.36	−2.27	−1.52 to −0.11	5.35	1	0.021*

*The symbol * refers to p-value < 0.05; the symbol *** refers to p-value < 0.001.*

differed among sexes, with males starting the experiment with similar latencies for the two types of food and ending up with shorter latencies for the novel food than for the familiar food, and females showing shorter latencies for the novel food throughout the whole experiment (**Figure 4**). *Group* was another significant control ($p = 0.020$; **Table 4**), with the longest latencies observed in group 4. In model M4, we detected moderate collinearity of *experience* and *age* (VIF = 6.6 and 6.4, respectively). We, thus, re-fitted the model after excluding age from the predictors, but the results did not change appreciably.

The full-null model comparison for M5 was highly significant ($\chi^2 = 55.11$, $df = 15$, $p < 0.001$). None of the 3-way interactions tested was significant. Similar to M4, the final model M5 contained a significant term for the interaction of *rank* and *food type* ($p < 0.001$; **Table 4**). To enhance comparison with M4, we retained the interaction of *session number* and *food type* despite it being non-significant at $\alpha = 0.05$ ($p = 0.074$), but all of the following also applied when this interaction was downgraded (not shown). *Risk attitude* was found to be a significant predictor of latency times ($p = 0.002$), which was shorter for more risk-prone subjects (**Table 4**), but this was not different for novel and familiar food (non-significant interaction of *risk attitude* and *food type*). However, in contrast to M4, M5 revealed a significant effect of the interaction of *experience* and *food type* ($p = 0.008$; **Table 4**), corresponding to higher neophobia in less experienced subjects. To check whether the differences between results of M4 and M5 were due to the inclusion of *risk attitude* as a predictor or the absence of *group*, *age* and *sex* as controls in M5, we proceeded as with M2 and M1. Again, the interaction of *experience* and *food type* was still significant in a model equivalent to (final) M5 without *risk attitude* among predictors (M5a: $\chi^2 = 6.700$, $df = 1$, $p = 0.010$), but obviously non-significant in a similar model applied to the complete data set (M5b: $\chi^2 = 0.424$, $df = 1$, $p = 0.516$), thus indicating that neither the inclusion of *risk attitude* nor the removal of *group*, *age* and *sex* were responsible for the difference between results of M4 and M5 and that the statistically significant interaction of *experience* and *food type* is an idiosyncratic feature of the smaller dataset used to fit M5. Indeed, checking for influential cases (see section "Materials and Methods") showed that the final model fitted on a subset of data excluding observations from Sandokan (**Table 1**) revealed a clearly outlier (much lower than the estimate for the final model) and a non-significant value for the coefficient of the interaction of *experience* and *food type*.

DISCUSSION

In this study, we tested neophobic response toward novel food in 23 captive capuchin monkeys. When neophobia was measured in terms of the *preference* (relative probability after controlling for availability) to retrieve familiar over novel food, we did not observe a clear bias in favor of the familiar food items in the first 10 retrieval episodes for each individual and condition (model M1; **Table 2** and **Figure 1**). Actually, a neophobic response does not necessarily imply an overall preference for retrieving familiar food items rather than novel food items. The relative preference for retrieving one or the other type of food may be seen as resulting from the combination of the overall attractiveness of each of the food items and the potential neophobic response against the novelty. As neophobia concerns a bias against novelty *per se*, the presence of a neophobic response can straightforwardly be revealed by a decrease in the relative preferences for familiar food over novel food as the subjects become acquainted with the novel food, which we modeled by an interaction of food type (familiar or novel) and number of retrieved items in models M1 and M2. Our analyses, however, did not reveal this interaction to be significant. Therefore, as long as the relative *preference* for retrieving familiar over novel food is concerned, we did not find clear evidence of a neophobic response. Conversely, in terms of *latency* to retrieve food, we observed the kind of significant interaction (in that case, between food type and session number) predicted by a neophobic response, with latency to retrieve novel food decreasing throughout the experiment, and latency to retrieve familiar food approximately constant over time (**Figure 4**). The better performance of analyses of *latency* over those of *preference* to retrieve food in revealing neophobia may, at least in part, depend on the more straightforward statistical modeling that can be applied to (log-transformed) latency times, which may be effectively modeled as a normally-distributed response in a linear (mixed) model. *Preference* for familiar over novel food, conversely, is better modeled as a probability that asymptotically converges to an arbitrary value (reflecting the relative palatability of each food type) and approximating it by a binomial GLMMs may not be ideal (despite we attempted to overcome this limitations by only analyzing pre-convergence observations, see section "Materials and Methods").

Our results provided no clear support to the hypothesis that previous experience generally decreases the neophobic response toward novel food. In fact, we did not find evidence that previous experience with experiments involving the presentation of unfamiliar food was related to a lower neophobia toward novel food items, in terms of either the probability or in the latency to retrieve familiar over novel food. These results are in contrast with findings showing that individuals with previous experience with novel stimuli, food or predators, have lower levels of neophobia when exposed to other types of novel food or predators (food: Catanese et al., 2012; predators: Ferrari et al., 2015; Crane and Ferrari, 2017). Indeed, it has been suggested that reduction of neophobia associated with previous experience with novelty is limited to very specific contexts (e.g., Bannier et al., 2017). However, we deem unlikely that our results may depend on a lack of context-specificity, because we measured "experience" specifically in terms of past exposure to experiments involving novel food (some of which with rather similar stimuli, **Supplementary Table 1**). On the contrary, we might speculate that generalization in capuchins is actually *less* context-specific than suggested by Bannier et al. (2017) in a fish model. In this view, as the captive capuchins involved in this study were all exposed to a variety of experimental conditions in the course of their lives, they could have all accumulated a "saturated" level of experience with novelty, making our measure actually irrelevant. Moreover, all the experiments with unfamiliar food, that we considered as part of subjects' experience, were performed many years before the current study; thus, their effect may have been diluted over time. Future studies should include more detailed

TABLE 4 | For models M4 and M5, test predictors and controls (in italics) included in the final model, estimates, standard errors (SE), *z*-values (*Z*), confidence intervals (CIs), likelihood ratio test's χ^2 (LRT), degrees of freedom (*df*) and *p*-values.

M4: neophobia as (log-transformed) latency time to retrieve familiar *vs.* novel food (Gaussian)

Term	Estimate	SE	*Z*	2.5 to 97.5% CI	LRT	*df*	*P*
Intercept	0.64	0.28	2.31	0.10 to 1.18	–	–	–
Experience	0.02	0.20	0.09	−0.37 to 0.40	0.01	1	0.931
Food type	0.57	0.17	3.33	0.23 to 0.90	–	–	–
Session number	−0.23	0.07	−3.21	−0.36 to −0.09	–	–	–
Rank	−0.27	0.12	−2.28	−0.50 to −0.04	–	–	–
Session number: food type	0.19	0.09	2.03	0.01 to 0.37	4.11	1	0.043*
Rank: food type	−0.58	0.12	−4.84	−0.82 to −0.35	22.96	1	<0.001***
Sex: food type	−0.84	0.24	−3.45	−1.32 to −0.36	11.73	1	<0.001***
Sex (male)	−0.46	0.27	−1.72	−0.99 to −0.07	–	–	–
Age	0.05	0.19	0.28	−0.32 to 0.43	0.08	1	0.777
Condition (B)	−0.05	0.11	−0.51	−0.26 to 0.15	0.26	1	0.611
Group	–	–	–	–	9.85	3	0.020*
Group (2)	0.29	0.28	1.02	−0.27 to 0.85	–	–	–
Group (3)	−0.21	0.26	−0.81	−0.72 to 0.30	–	–	–
Group (4)	0.63	0.23	2.73	0.18 to 1.09	–	–	–

M5: neophobia as (log-transformed) latency time to retrieve familiar *vs.* novel food (Gaussian), including risk attitude

Term	Estimate	SE	*Z*	2.5 to 97.5% CI	LRT	*df*	*P*
Intercept	0.51	0.22	2.35	0.46 to 0.91	–	–	–
Experience	−0.32	0.12	−2.54	−0.56 to −0.07	–	–	–
Food type	−0.41	0.13	−3.22	−0.66 to −0.16	–	–	–
Session number	−0.31	0.09	−3.40	−0.48 to −0.13	–	–	–
Rank	0.15	0.10	1.45	−0.05 to 0.36	–	–	–
Risk	−0.35	0.09	−3.95	−0.52 to −0.18	9.10	1	0.002**
Experience: food type	0.37	0.14	2.66	0.10 to 0.64	6.95	1	0.008**
Session number: food type	0.23	0.13	1.79	−0.02 to 0.47	3.17	1	0.074
Rank: food type	−0.52	0.14	−3.70	−0.79 to −0.24	13.28	1	<0.001***
Condition (B)	0.17	0.13	1.37	−0.07 to 0.42	1.88	1	0.170

*The symbol * refers to p-value < 0.05; the symbol ** refers to p-value < 0.01; the symbol *** refers to p-value < 0.001.*

measures of individuals' previous experience with novelty, and better assess how such experience might affect response to novelty in a variety of different contexts (Ferrari et al., 2015; Bannier et al., 2017; Crane and Ferrari, 2017). However, it is possible that the stimuli we presented were not novel enough to the study subjects, reducing our ability to detect the effect of previous exposure to novelty on neophobia, or that the capuchins' long habituation to being fed in captivity made them perceive any food presented as essentially harmless. In other words, regardless of their specific previous experience with novel food, capuchins may have perceived the "novel" bananas as being rather familiar or, anyway, benign, thus showing overall little neophobia. This interpretation is consistent with the small (if any) bias in favor of familiar food that we have observed (**Figure 1**). Finally, we must note that our analysis of the reduced dataset including the 8 individuals with risk-attitude data did actually reveal statistical significance for the effect of the interaction between experience and food type on latency times (model M5, **Table 4**), suggesting that neophobia was lower in subjects with more previous experience. As the same result was not confirmed by the analysis of the whole data set, we cannot consider this as sufficient evidence, but it suggests that the relation of primates' neophobia with past experience in a feeding context deserves further investigation. We also found no support to the hypothesis that risk-proneness is linked to lower neophobia, as we did not find differences in the relative preference for familiar over novel food associated with previous measures of individuals' risk attitude (model M1, **Table 2**), nor a significant effect of the interaction between risk attitude and food type on latency to retrieve food (model M5, **Table 4**). Since novelty is associated with uncertainty, it is reasonable to expect risk-proneness (i.e., the preference for riskier over safer options; De Petrillo et al., 2015) to be associated with low neophobia. Most of the studies that found an association of neophobia with risk, however, have investigated neophobic responses in dangerous situations, as predation (fishes: Brown et al., 2013; Brown et al., 2016; review in Crane and Ferrari, 2017) or anthropogenic disturbance (birds: Bókony et al., 2012; Greggor et al., 2016), suggesting that being exposed to a risky situation induces neophobia (e.g., predator avoidance; Brown et al., 2013). It is possible that the way in which we operationalized risk attitude (i.e., propensity to seek a randomly varying reward over a more predictable one) simply

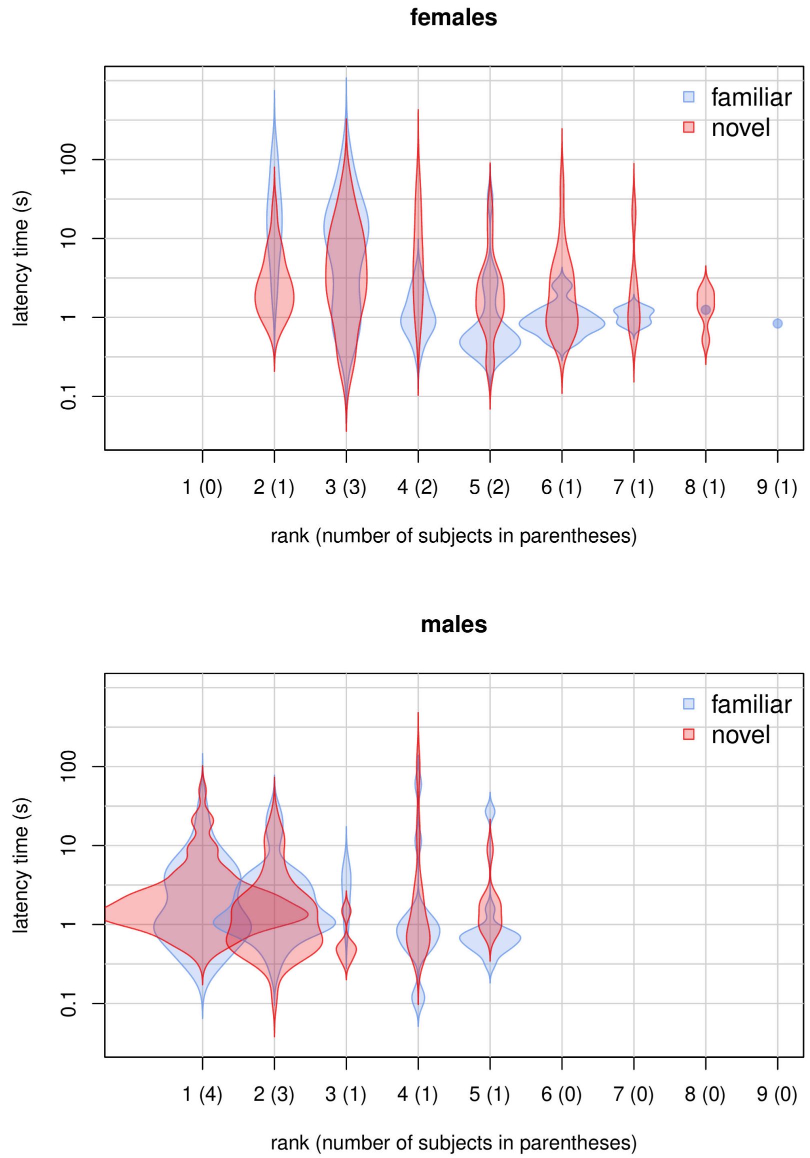

FIGURE 3 | Violin plots showing the distribution of latency times for novel and familiar food items for each rank and sex.

does not mirror the uncertainty that is instead linked to novelty, when subjects lack any information about the possible payoffs associated with novel stimuli (see Paglieri et al., 2014). However, as risk-attitude scores were available for only 8 out of our 23 subjects, low sample size certainly limited our power to detect a link between risk attitude and neophobia. Future studies should investigate the relationship between risk attitude and neophobia using different measures of risk proneness and including a larger sample of individuals.

We did not find that individuals reversed their food preferences in the presence of higher-ranking group members, nor that the presence of other conspecifics affected individuals' preference for familiar over novel food (model M1, full-null not significant, **Table 2**). This result seems to be in contrast with other studies showing that the presence of a conspecific facilitates the acceptance of novel food in primates (Visalberghi and Addessi, 2000, 2001; Addessi and Visalberghi, 2001; Addessi et al., 2007; Hardus et al., 2015; Englerova et al., 2019). In these studies, however, conspecifics were not directly in contact with the focal subject (i.e., they had only visual but not physical contact). Therefore, the presence of conspecifics may decrease neophobic response, although only in a non-competitive context, in which individuals do not have access to the same food resources (but see Visalberghi and Fragaszy, 1995).

We found that several aspects of sociality were linked to neophobia. First, in agreement with the literature (Ellis, 1995; Altmann, 1998; Hohmann et al., 2006), higher-ranking monkeys had priority of access to resources, participating more than

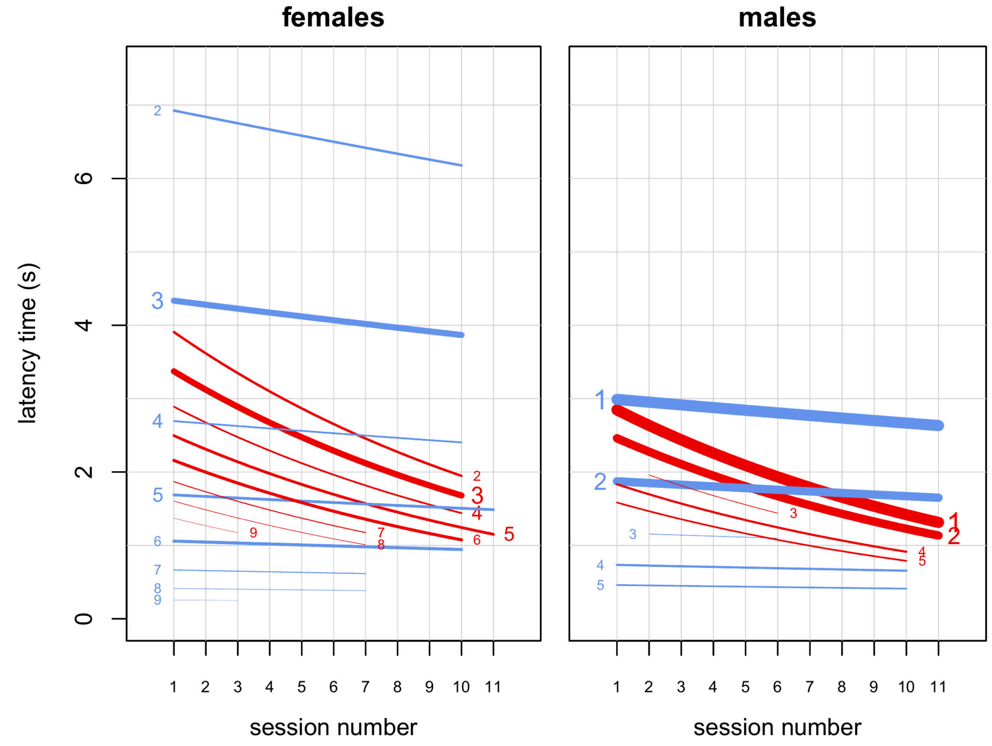

FIGURE 4 | Results from model M4. Interactions of sex, rank and session number with food type (familiar or novel). Lines represent estimated latency times as a function of session number for novel (red) and familiar (blue) foods and different ranks, indicated by numbers on the right (for novel) or left (for familiar) of each line. The plot on the left concerns females, while the plot on the right concerns males. All other predictors were kept at their sample mean. Line width is proportional to the number of observations for each combination of food type, rank and sex. Lines extend from the minimum to the maximum session number for each combination of food type, rank and sex. Font size of numbers indicating rank is proportional to the number of subjects in each rank in the study sample. Latency time is generally shorter for low-ranking individuals and latency time for novel food decreases markedly from early to late sessions.

lower-ranking individuals in our experiment (model M3; **Table 3** and **Figure 2**). Moreover, participation decreased for lower-ranking individuals (**Figure 2**), suggesting that, as all subjects familiarized with the experimental setup, higher-ranking individuals strengthened their control over the provided food. Then, in contrast to what reported by Crane et al. (2020), our data indicated separate detectable effects of rank and sex on latency times (model M4; **Table 4** and **Figure 4**). Higher-ranking individuals showed generally longer latency to retrieve food (both familiar and novel) than lower-ranking ones, probably because the former do not need to be quick in order to outcompete conspecifics (**Figures 3**, **4**). Notably, lower-ranking individuals typically retrieved their first food item in about one second or less (**Figures 3**, **4**). Moreover, higher-ranking individuals appeared generally less neophobic than lower-ranking ones, showing a stronger bias toward a quicker retrieval of the familiar food than the novel food. Based on results from model M4, we estimated that, in the earliest sessions of the experiment, lower-ranking subjects (females ranking $\geq$ 5 and males ranking $\geq$ 2) retrieved the familiar food more quickly than the novel food (**Figure 4**), while, for higher-ranking individuals, there was no such a clear trend (higher-ranking females tended to retrieve the familiar food more slowly than the novel food, and higher-ranking males had similar times for both types). Toward the end of the experiment, higher-ranking monkeys (both females and males) retrieved the novel food more quickly than the familiar one and it seems reasonable that they learned to appreciate the texture and small added nutritional value provided by the seeds covering the "novel" banana slices (Addessi et al., 2004). Rank and session number being equal, latency times for females were significantly longer than for males when both retrieved familiar foods, while the effect of sex on latency times to retrieve novel food was much smaller (**Figure 4**). This observation may indicate that, at least in this captive population, female capuchins are actually less neophobic than males (in line with a study on wild capuchin monkeys; Visalberghi et al., 2003a; but in contrast to Crane et al., 2020). However, given that this effect seems to be driven by the longer times female took to retrieve familiar items, rather than by their quicker retrieval of novel items, it is still possible that this sex difference actually depends on other social aspects of the feeding behavior of males and females which could not be revealed by our measures. Overall, these results suggest that individuals flexibly adjust their behavior when tested in a social context, while it does not clearly support the idea that lower-ranking individuals preferentially retrieve the food that reduces occasions for competitive interactions (Gomez-Melara et al., 2021). On the one hand, we did not observe a significant effect of rank difference (presence of higher ranking individuals) on preference for familiar over novel food (model M1, **Table 2**). On the other hand, if differences in latency to food retrieval can be taken as an alternative measure of preference, we would expect that, as higher-ranking individuals shifted more toward novel food over the course of the experiment, lower-ranking individuals did the opposite, which was not the case (**Figure 4**).

An arguably odd feature of our study was the observation of statistically significant effects of interactions involving previous experience with novel food in the reduced data set comprising those monkeys with risk-attitude scores available. None of these effects could be confirmed in the complete data set, and our checks seem to indicate that they were indeed idiosyncratic features of the subsets of data used to fit models M2 and M5, comprising observations from eight subjects. Those eight individuals belonged to all four social groups and included all of the dominant males plus four females that are known to be particularly willing to participate in experiments, and may represent a sample that is not entirely representative of the whole colony. Interestingly, the distribution of experience with novel food in this data set is relatively unbalanced, with two subjects that have not been involved in previous experiments (experience = 0) and the remaining six individuals having performed from four to eight experiments. At least in the case of model M5, the influence of a single individual was clearly decisive while, for model M2, there was no such an obvious explanation. While it is difficult to determine if and how the peculiar features of each data set may drive to statistically significant signals that cannot be straightforwardly generalized, this finding highlights the difficulty to generate robust and general conclusions about inter-individual as well as inter-and intraspecific behavioral patterns. We, therefore, strongly embrace the call for investigating individual differences and its causes in animal cognition possibly through large, collaborative open-science projects (e.g., Thornton and Lukas, 2012; Many Primates et al., 2019).

Although our study failed to confirm our main predictions, its findings contribute to our understanding of individual variation in primate response to novelty. Future research should extend the study of neophobia in social settings, by using a larger variety of social contexts with different levels of competition over food, in order to monitor how the presence of conspecifics affects changes in the individual response to novelty. Moreover, it would be interesting to use a larger variety of novel stimuli, to systematically address how primates generalize previous experience and novelty depending on the specific characteristics of the stimuli they are exposed to. A better understanding of how animals respond to novelty will provide us with crucial information about their ability to respond to novel socio-ecological challenges and, importantly, it will have ethical implications, by contributing to improve the welfare of captive animals (Buchanan-Smith, 2011), to increase the effectiveness of reintroduction programs (Hardus et al., 2015), and to carry out more effective conservation programs in habitats where rapid environmental changes arise (e.g., in deforested or urbanized environments; McLennan et al., 2017) resulting in animals facing more frequently the necessity to switch over novel food sources for their survival.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

The animal study was reviewed and approved by Italian Health Ministry (DM 633/2020-PR to GSi).

AUTHOR CONTRIBUTIONS

MV, GSa, EA, and GSi contributed to the design of the study. MV, GSa, and GSg contributed to data collection. MV organized the database. PG performed the statistical analyses. MV and PG drafted the manuscript. All authors contributed to the final writing of the manuscript and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.820323/full#supplementary-material

Supplementary Figure 1 | Structure of the enclosure and experimental setting. Food items (banana slices) were provided in both indoor areas, connected through sliding doors to the outdoor area of the enclosure. Yellow circles indicate the familiar bananas, blue circles indicate the novel bananas in condition A (i.e., blue banana slices with sesame seeds). Food items were as evenly distributed as possible while ensuring visibility from the point of view of recording cameras.

Supplementary Table 1 | List of studies on individual reaction to novel food and, in the last line, on risk attitude, which have been carried out at the Primate Centre of the ISTC-CNR, Rome, Italy.

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Life in 2.5D: Animal Movement in the Trees

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The complex, interconnected, and non-contiguous nature of canopy environments present unique cognitive, locomotor, and sensory challenges to their animal inhabitants. Animal movement through forest canopies is constrained; unlike most aquatic or aerial habitats, the three-dimensional space of a forest canopy is not fully realized or available to the animals within it. Determining how the unique constraints of arboreal habitats shape the ecology and evolution of canopy-dwelling animals is key to fully understanding forest ecosystems. With emerging technologies, there is now the opportunity to quantify and map tree connectivity, and to embed the fine-scale horizontal and vertical position of moving animals into these networks of branching pathways. Integrating detailed multi-dimensional habitat structure and animal movement data will enable us to see the world from the perspective of an arboreal animal. This synthesis will shed light on fundamental aspects of arboreal animals' cognition and ecology, including how they navigate landscapes of risk and reward and weigh energetic trade-offs, as well as how their environment shapes their spatial cognition and their social dynamics.

Keywords: arboreal mammals, foraging, decision-making, navigation, forest

INTRODUCTION

Forests cover over 30% of the world's land area, and support the vast majority of land-based animal species (FAO and UNEP, 2020). In tropical forests, approximately 50–90% of vertebrates, and up to 75% of mammals, representing hundreds of species, make use of arboreal substrates (Kays and Allison, 2001; Malcolm and Lowman, 2004). Forest canopies are complex, dynamic, three-dimensional networks of intertwined branches and vines connecting at variable heights and angles, and with variable strengths and spacing. Because arboreal animals are generally constrained to moving along these substrates, the full three-dimensional space of the canopy is not available to them; they live their lives in "2.5D." Canopy-dwelling animals (that do not fly) therefore face cognitive, locomotor, and sensory challenges that are not shared by ground-dwelling animals, nor by most aerial or aquatic animals whose substrates (air and water) are continuous in three-dimensional space. Exactly how the unusual 2.5D properties of forest canopy habitats shape the lives of the animals that inhabit them has been difficult to study, largely due to the inaccessibility of these treetop habitats to bipedal human observers.

Technological advances are poised to provide a new window through which we can observe and study arboreal species in their canopy habitat. Ground, aerial, and satellite-borne scanning technologies can produce digital reconstructions of complex forest habitats, allowing for the quantification and mapping of canopy branch networks. Combining multiple data-logging devices into small, wearable, on-animal sensors allows for the fine-scale tracking of animal movement in three dimensions. Cutting-edge computational modeling and virtual reality technologies now allow us to integrate these data streams—detailed habitat structure and animal movement data on both the horizontal and vertical axes—making it possible for us to see the world from the perspectives of arboreal animals. The development and refinement of these technologies is opening new avenues of study, and allowing us to ask new questions about how the unusual aspects of arboreal habitats shape the decision-making of canopy-dwelling animals.

A VIRTUAL WINDOW INTO A 2.5D WORLD

Forest canopies, and especially tropical rainforest canopies, are complex and dynamic networks of diverse trees and lianas. From the ground, we see a dense tangle of branches, vines, and epiphytes; it is nearly impossible to decipher where one plant ends and another begins. While these forests consist of multiple strata (Hallé et al., 2012)—layers that can be used to classify vertical patterns of vegetation and biodiversity—their boundaries are blurry and often indifferentiable from below. From above, we can see the irregular height of the forest canopy, with emergent trees reaching above a lower, denser layer of leafy canopy, but we are blind to the branching structures hidden below. Forests are dynamic, ever-changing, environments; branches break and fall, lianas and epiphytes get dislodged, trees die and eventually topple over—often pulling down, or crushing, others along the way (Cushman et al., 2022). From our boots on the ground, or our seats in the sky, we cannot fully appreciate, let alone accurately quantify or map, the complex structure of these arboreal habitats.

Technological advances allow for increasingly accurate and detailed mapping of complex canopy habitat structure. Light Detection and Ranging (LiDAR) systems can map the three-dimensional architecture of forests (Davies and Asner, 2014; Rodríguez-Ronderos et al., 2016; McClune, 2018; Moorthy et al., 2019), and when mounted on a drone or a plane, offer promising opportunities for balancing fine-scale and landscape-level measurements of tree and forest structure, canopy height, and vegetation density (Asner et al., 2008). Satellite-borne LiDAR systems can also measure vertical canopy structure at larger spatial scales, although with coarser resolution (e.g., Global Ecosystem Dynamics Investigation, GEDI) (Dubayah et al., 2020; Lang et al., 2021). Future advances that allow for higher spatial- and temporal-resolution forest and canopy structure data to be collected from satellites will enable the quantification and mapping of canopy structure over wider and longer scales. Although analytical challenges remain in moving from the point-clouds produced by LiDAR systems to full and robust representations of the three-dimensional networks of branches and lianas that connect the forest canopy (Okura, 2022), it is likely that we will, in the near future, have the ability to recreate detailed maps of these environments.

The parallel challenge is to situate animals and their movements within these detailed canopy maps (McLean et al., 2016; Davies et al., 2017). Unlocking the ability to precisely measure the vertical axis of movement is critical to this endeavor; current tracking of forest animals is largely confined to two dimensions, focusing on animal locations and tracks on the horizontal plane (e.g., Crofoot et al., 2010). There are technological hurdles to obtaining accurate, fine-scale vertical position data, but progress is being made. Vertical positioning signals can be extracted from GPS (**Figure 1B**), and can be used to assess questions about canopy use at gross scales (Thiel et al., 2021, e.g., niche stratification; **Figure 1C**), but may be too noisy to look at fine-scale movement decisions (Péron et al., 2020). Because the vertical axis of movement in a forest canopy is relatively limited—mean forest heights rarely exceed 40 m (Lefsky, 2010)—more precision is required to obtain relevant measures of vertical position for forest-dwelling animals than for many aerial and aquatic species, where three-dimensional tracking is already often used (e.g., Wilson et al., 2007; Bestley et al., 2015; Nagy et al., 2018). Barometers, by tracking air pressure, can detect small changes in height above ground, although calibration with nearby ground-station measurements is needed to account for weather-induced changes in air pressure (Sjöberg et al., 2018). Accelerometers, magnetometers, and gyroscopes can be used for dead reckoning, i.e., the fine-scale reconstruction of an animals' movement paths through three dimensions (Bidder et al., 2015). The fusion of these data streams holds incredible promise for measuring the vertical axis of animal movement at the fine-scale that is needed for canopy-dwelling species. To date, this has not yet been attempted for arboreal species, but it is a promising avenue for future development.

The question then becomes, "How can we use these data to develop and test meaningful hypotheses about the behavior and ecology of arboreal animals?" The solution may lie in virtual reality (VR), where emerging technologies are offering new avenues through which we can embed animals' movement trajectories into reconstructions of their canopy habitat's branching systems, and then not only "see" the choices that animals make but also "observe" counterfactuals, i.e.,

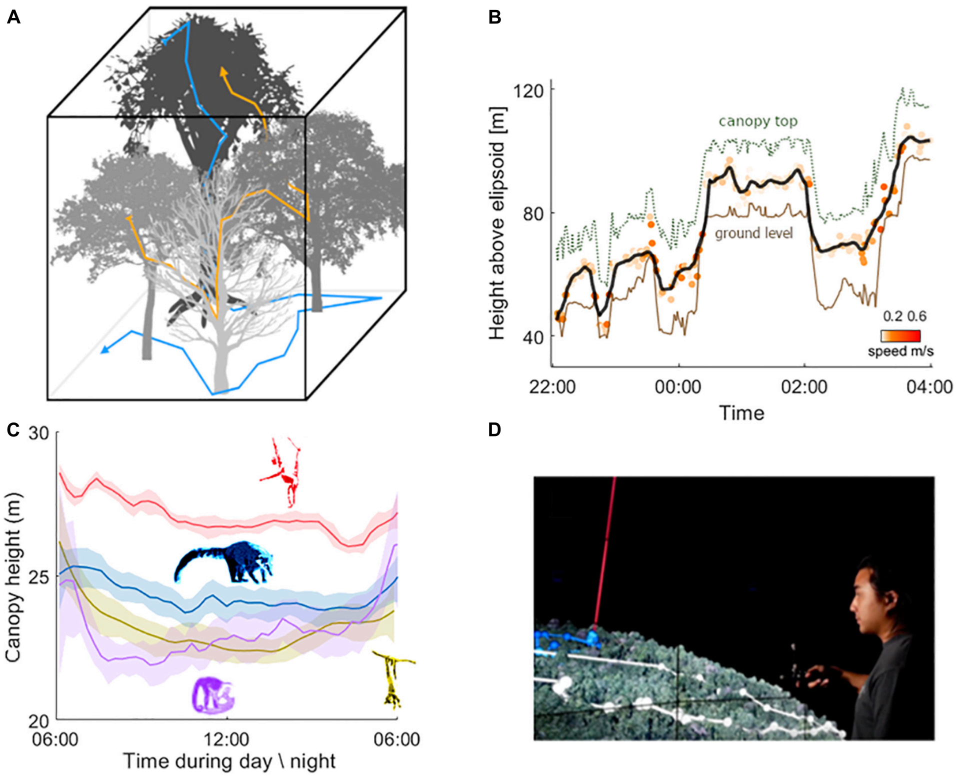

FIGURE 1 | A virtual window into a 2.5D world. **(A)** Integrating three-dimensional animal movement tracks with the mapping of these complex three-dimensional habitats, will enable us to study how animals navigate the branching structures of their arboreal environments. **(B)** Vertical movement track over time of an arboreal kinkajou (*Potos flavus*) in reference to ground (brown solid line) tracked on Barro Colorado Island, Panama, and canopy height (green dashed line). GPS data were sampled at 1 Hz and dots represent 1-min median values. The solid black line represents a running median of the height measurements over a 15-min interval. **(C)** Based on the animal's horizontal movements we can extract where in the canopy animals move over the course of the day. Spider monkeys (*Ateles geoffroyi*, red) tend to stay in higher canopy areas, while coatis (*Nasua narica*, blue), capuchins (*Cebus capucinus*, purple), and kinkajous (yellow) move through areas with lower canopy heights. The averages (and 95% CI shading) over the active period for four arboreal mammals species: coati (blue, *N* = 17 individuals), kinkajou (purple, *N* = 13 individuals), capuchin (yellow, *N* = 8 individuals), and spider monkey (red, *N* = 8 individuals) are presented. Each line represents the cumulative average values smoothed over 15-min of the individuals of a single species during the activity time of the individuals. Sources of DEM (digital elevation model) and canopy height data (Havmøller et al., 2021). Coatis sleep high in trees and descend to the ground in the mornings, forage on the ground during the day to return up into the trees at night (Kaufmann, 1962). Kinkajous and capuchins stay within the canopy and are known to only rarely come to the ground. Spider monkeys spend the majority of their day high in the canopy and have the least overall variation in vertical positioning. **(D)** Sensei-Panama visualization in CAVE2, visualizes animal movement trajectories within a virtual tropical environment, reconstructed from sensor and image data. Animal movements are shown with points connected by lines.

the options that were available but not chosen. For example, the "Sensei-Panama" application at the CAVE2 facility in the Electronic Visualization Laboratory, University of Illinois Chicago, allows observers to "fly through" a VR visualization of the 1560-ha tropical forest on Barro Colorado Island in Panama, reconstructed from depth-from-motion drone data and high-resolution aerial image data (Aurisano et al., 2019; **Figure 1D**). Within this virtually-reconstructed landscape, we can visualize the movement trajectories of GPS-tracked animals from the animal's own point of view by "moving" along animal GPS tracks through the canopy. We can thus qualitatively and quantitatively assess our study animals' movement decision-making, from their own points of view. Integrative and cutting-edge VR approaches need not be so large-scale and infrastructure-intensive, however. VR headsets are becoming increasingly accessible and powerful, and the democratization of this technology will enable its more widespread implementation.

UNDERSTANDING ANIMAL DECISION-MAKING IN A 2.5D WORLD

The 2.5D nature of the forest canopy shapes many facets of arboreal animals' lives. Integrating three-dimensional animal movement tracks with the mapping of these complex three-dimensional habitats (**Figure 1A**), will enable us to explore a whole new dimension of key questions related to animal navigation, cognition, and the mechanisms that underlie movement decisions.

How Do Animals Navigate the Vertical Distribution of Risk and Reward?

The vertical structuring of canopy habitats can have significant bearing on the spatial distribution of nutritional rewards. The nutritional quality of leaves (chlorophyll content) and fruits (sugar and protein content) is often higher where sun exposure is higher (Houle et al., 2014; Rothman et al., 2015), making the top of the canopy and forest edges desirable foraging areas. The potential benefits of accessing particular resources must, however, be weighed against potential costs, including predation risk (Gaynor et al., 2019), which also varies with height in the canopy; animals are more vulnerable to aerial predators when in high exposed areas, and to ground-dwelling predators when descending to the ground (Shultz et al., 2004; Makin et al., 2012). From studies focusing on two spatial dimensions, we know that animals' movement is heavily influenced by the combined pressures of their landscapes of fear and the spatio-temporal distribution of important resources, such as food and nesting sites (Willems and Hill, 2009; Willems et al., 2009). But how do these competing forces interact with 2.5D environmental considerations—such as the animal's height above ground, and the surrounding canopy branching structure—as well as energetic and safety considerations, to influence animal movement in three-dimensions? When and where do animals choose to climb higher, into more exposed areas (potentially increasing their risk of aerial predation) in order to access nutritionally higher-quality food sources? Similarly, are animals more likely to descend lower (potentially increasing their risk of ground-based predation) around forest edges or canopy gaps than elsewhere, to access unique resources that are only available—or that are more nutritious—in these boundary areas?

Arboreal animals must also consider the safety risks associated with potentially falling. While some travel route options may be more direct (i.e., energy- and time-efficient) and some foraging locations maybe more valuable (i.e., allow access to more nutrient-dense resources) they may present higher safety risks, such as a higher risk of falling from needing to jump across gaps or from relying on smaller and weaker branches (Pontzer and Wrangham, 2004). Evidence suggest that safety considerations have a strong effect on animal movement decisions: during vertical climbing, primates slow down and attempt to increase stability (Granatosky et al., 2019); and in species where canopy gaps are often navigated by jumping, larger-bodied individuals are more likely to choose an energetically expensive mode of circumventing canopy gaps (e.g., an indirect route) rather than risk jumping (Halsey et al., 2016). Furthermore, humans' energetic costs while climbing are comparable to those of other animals, suggesting that morphological adaptations to arboreality may be the result of selection for safety, rather than energetic efficiency (Kozma and Pontzer, 2021). When and where do arboreal animals choose "riskier" travel pathways, and how does this vary between individuals, groups, and species? Species and individuals vary in their abilities to move across, over, under, and between different sizes, angles, rigidities, and strengths of arboreal substrates. Thus, the degree of risk incurred, and the energetic and time costs of travel, can be extremely variable—depending on the individuals and species, but also the structure of the habitat through which they are moving (Granatosky, 2018; Wheatley et al., 2021). How does variation in animals' body characteristics (e.g., body size, limb length) and locomotor styles (e.g., quadrupedalism, brachiation, and leaping), interact with substrate availability and connectivity (e.g., branch characteristics and gap sizes) to shape locomotor choices, such as when to walk, leap, swing, reach or sway (e.g., Emmons and Gentry, 1983; Graham and Socha, 2020)?

Where ground-based predation pressure is comparatively low, such as predator-free islands, animal species that are elsewhere confined to the trees, may spend relatively more time on the ground (Ashbury et al., 2015; Monteza-Moreno et al., 2020)—suggesting that ground-use and ground-travel may have important benefits (e.g., access to particular nutritional resources, and energetically-efficient and safe travel). Indeed, ground-travel may be an energetically cheap option—especially for larger-bodied animals (Hanna and Schmitt, 2011)—that allows for direct navigation without any risk of falling (Janson, 1988). Conversely, in some cases, traveling through the canopy may be significantly less energetically expensive than ground travel, such as when moving through the trees allows an animal to buffer the effects of topography (e.g., when crossing ravines or narrow saddles), or when leveraging the biomechanical energy of compliant trees and branches (e.g., orangutans tree-swaying, Thorpe et al., 2007). Integrating the paradigms of energy landscapes and landscapes of fear into the three-dimensional study of arboreal animals' movement decisions is a promising approach for better understanding how animals weigh predation risk against energetic benefits (Gallagher et al., 2017; Williams and Safi, 2021).

How Does Incomplete Substrate Connectivity Shape the Way That Animals See and Think About the World?

Arboreal animals face cognitive challenges that are specific to moving through the canopy. Compared to their ground-dwelling counterparts, arboreal animals' cognitive maps may have to incorporate the vertical dimension—recognizing that the same location in horizontal space may look (and sound, and smell) very different at different heights in the forest. Adding to this potential cognitive challenge, in the trees, dense vegetation limits visual perception range (Janson and Di Bitetti, 1997). While this likely increases the importance of acoustic (Richards and Wiley, 1980), olfactory (Kuijper et al., 2014) cues, vegetation can be noisy enough to disrupt an animal's ability to hear, and locate the source of, surrounding sounds (Yip et al., 2017), and can disrupt an animal's ability to follow scent plumes due to high airflow turbulence (Garber and Hannon, 1993), and increase reliance on memory. Compared to animals that swim or fly, arboreal animals' cognitive maps must account for the discontinuous and dynamic nature of their substrates; their movement decisions are constrained to the discrete pathways offered by trees' and lianas' inter-connectedness, and viable pathways may shift, change, emerge, or disappear gradually or suddenly over time (Pretzsch, 2009; Cushman et al., 2022). Furthermore, many horizontal and vertical movement options may not follow linear paths that lead directly or immediately in the intended direction of travel (Juliani et al., 2016). How do these challenges and constraints shape the spatial cognition of arboreal animals? Do arboreal animals have comparatively well-developed attentional filtering, memory, and reasoning to enable flexible and efficient search and navigation (as per

Mueller and Fagan, 2008; Matzel and Kolata, 2010; Fagan et al., 2013)?

Animals might cognitively adapt to the constraints of an arboreal habitat by evolving an increased capacity for identifying local landmarks and repeating—through reinforcement learning—sequences of navigational decisions that result in efficient travel paths (Anggraini et al., 2018; Wu et al., 2021). Such adaptations would increase the ability to find and follow known, safe routes in the canopy without needing to keep track of the three-dimensional spatial relationships between those resources. Additional adaptations that aid in mentally modeling three-dimensional spatial relationships would improve an animal's ability to navigate flexibly in response to changing canopy structure. For example, if arboreal animals are to keep track of their own position relative to out-of-sight locations, doing so in an extra dimension may require a larger working memory capacity and higher attunement to their body's movement and position in space (proprioception) than that required by ground-dwelling animals (Heinze et al., 2018). Arboreal animals might also acquire spatially explicit information about the relationships between multiple locations by seeking out vantage points and integrating multiple perceptual vistas into a single cognitive map–behavior that would require some degree of meta-cognition and mental rotation of perceived scenes. Investigating the relationships between the connectedness and dynamism of animals' arboreal habitats, and certain key aspects of their movement behavior—such as their frequency of route-use and the timing of their spatial information-seeking behavior—will shed light on the strategies that arboreal animals use to cope with the cognitive challenges of living in forest canopies.

How Does Canopy Structure Shape Social Dynamics?

For group living species, the vertical component and branching structures of their arboreal environments may play an important role in foraging competition and social dynamics (Boinski, 1989; Williamson et al., 2021). Competition for resources may be shaped by, not only the abundance and distribution of the resources themselves, but also the availability of pathways by which to even *access* these resources, with more dominant individuals monopolizing the branches that are within reach of the best foraging patches. Vertical stratification of group members may allow for increased within-group resource partitioning, allowing individuals to remain in proximity with each other but avoid direct conflicts over feeding space (Houle and Wrangham, 2021). Vertical stratification of group members may also block line-of-sight and interfere with within-group information transfer (Webster et al., 2013). How does vertical stratification enable or inhibit group cohesion and coordination?

Group cohesion and social interactions, while traveling, foraging and resting, may also be shaped by the structure of the forest canopy. The benefits of maintaining cohesion and engaging in these affiliative interactions with group-mates must be weighed against the safety of congregating in different canopy locations and the ability of all group members—including larger-bodied and heavier individuals, and individuals with reduced locomotor capacities, e.g., immatures—to access and move through these locations (as per del Mar Delgado et al., 2018; Jolles et al., 2020; Harel et al., 2021). How does variation in body size and locomotor capacity between individuals within a group, as well as the number of individuals in the group, interact with factors such as branch connectivity, strength and space, vulnerability to potential predators, access to resources, and the likelihood and potential severity of falling, to determine travel routes and congregation locations that are available to the group? Where a travel route or location is not accessible or safe for all group members, how are conflicts of interest handled?

CONCLUSION

The key to answering these questions lies in the development and integration of technological advances that enable detailed three-dimensional mapping of canopy habitat structure and arboreal animals' movements on a very fine spatio-temporal scale (Nathan et al., 2022). No technology can compete with the richness of direct observation, but—particularly in cases where observation, or at least detailed quantification, is not possible—remote sensing technologies have a unique role to play in letting us see worlds that we could not otherwise see. Careful attention needs to be paid to how these technologies—e.g., on-animal collars, or low-flying drones—may influence the very behaviors we seek to study. With careful and ethical implementation, these emerging technologies will enable us to develop and reliably test meaningful hypotheses specific to the ecology, behavior, and cognition of canopy-dwelling animals.

Living in constrained three-dimensional environments is likely not unique to canopy-dwelling animals; animals that depend heavily, for example, on coral reefs and underground tunnels may face many similar challenges associated with complex and constrained three-dimensional habitats. Many aerial and aquatic species may also face movement constraints in their habitats, as the invisible structuring of currents in open air and aquatic environments may heavily influence the actual movement path choices that are available to them. By developing and integrating technologies that allow for the fine-scale reconstruction of complex habitats—be it forests or other—as well as the tracking of animal movement, we can achieve an animal's-eye view of the challenges and choices associated with living in 2.5D.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. Data are available upon request at "Movebank" (www.movebank.org).

ETHICS STATEMENT

The Institutional Animal Care and Use Committees (IACUC) at the Smithsonian Tropical Research Institute (protocol number 2014-1001-2017, 2017-0605-2020, and 2017-0912-2020) and the University of California, Davis (protocol number 18239) approved all animal handling and collaring procedures.

AUTHOR CONTRIBUTIONS

MC, RK, BH, KM, and RH formulated the idea. RWH, MC, BH, and RK collected data. RH, AA, and CN prepared the figures. RH, AA, and MC lead the writing. All authors contributed to the text.

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The primate workplace: Cooperative decision-making in human and non-human primates

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The success of group foraging in primates is not only determined by ecological and social factors. It is also influenced by cognition. Group foraging success is constrained, for instance, by the challenges of coordination, synchrony and decision-making, and it is enhanced by the ability to share, learn from others and coordinate actions. However, what we currently know about the cognition of individuals in groups comes primarily from experiments on dyads, and what we know of the effect of ecological factors on group dynamics comes from larger wild groups. Our current knowledge of primate group behaviour is thus incomplete. In this review, we identify a gap in our knowledge of primate group dynamics between the dyadic studies on primate cooperation and the large group observational studies of behavioural ecology. We highlight the potential for controlled experimental studies on coordination and cooperation in primate groups. Currently, these exist primarily as studies of dyads, and these do not go far enough in testing limits of group-level behaviours. Controlled studies on primate groups beyond the dyad would be highly informative regarding the bounds of non-human primate collaboration. We look to the literature on how humans behave in groups, specifically from organisational psychology, draw parallels between human and non-human group dynamics and highlight approaches that could be applied across disciplines. Organisational psychology is explicitly concerned with the interactions between individuals in a group and the emergent properties at the group-level of these decisions. We propose that some of the major shortfalls in our understanding of primate social cognition and group dynamics can be filled by using approaches developed by organisational psychologists, particularly regarding the effects of group size and composition on group-level cooperation. To illustrate the potential applications, we provide a list of research questions drawn from organisational psychology that could be applied to non-human primates.

KEYWORDS

organisational psychology, coordination, collective decision-making, group dynamics, group foraging

Cooperating in groups

Cooperation, the proficiency with which primates can be said to cooperate, and the cognitive capacities needed for it, have been a particular focus of experimental studies (Visalberghi et al., 2000; Rekers et al., 2011; Stocker et al., 2020; Martin et al., 2021). Such studies have however focused on dyads rather than individuals embedded in larger social groups. There is, for example, only one study that experimentally tests cooperation in chimpanzees in groups larger than two (Suchak et al., 2016), which is surprising given most observed instances of possible cooperation in wild chimpanzees, hunting and coalitionary attacks, involve large groups. Results from human studies also indicate the dyad is a special case in regard to group dynamics. Zimet and Schneider (1969) found that dyads showed significantly less within-group aggression and significantly more within-group support as compared to other group sizes and that the difference between groups of two and three was much greater than between three and four. Nosenzo et al. (2015) found cooperation to be highest of all in two-person groups. There may be something unique about dyadic cooperation that makes studies testing groups larger than two even more important.

This review identifies a gap between the dyadic cooperation studies of cognitive biologists and comparative psychologists and the larger group observations of behavioural ecologists and primatologists; it recognises a need for experimental studies beyond the dyad to tell us more about individual social cognition in naturalistic groups, particularly group size effects on cooperation. The cognitive abilities necessary for individuals in large primate groups to make consensus decisions, coordinate activity budgets and movement and mitigate the numerous costs of social living are not well understood despite being particularly relevant to primates that forage in groups. Specifically, we are interested in what happens when individual or dyadic coordination problems are scaled up to the size of natural groups.

Accordingly, we provide an overview of primate group dynamics (both human and non-human); what differentiates individual from group behaviour, how group-level decisions are made, and what is known about coordinated action. We draw attention to the dearth of studies into group size effects on non-human primate group behaviour and provide an overview of such studies in human organisational psychology. In doing so we highlight where interests align and present opportunities for integration of approaches across disciplines. We also provide potential future research questions and discuss what we would expect these to find, as well as their relevance to wild primate food acquisition behaviours such as making coordinated movement decisions when foraging and engaging in group hunts.

Cooperation

Cooperation has a variety of definitions across different fields. An adaptive (biological) definition of cooperation is any behaviour that provides a fitness benefit to another and has evolved for this benefit to the recipient (West et al., 2007). In this review, we will however use a social interaction perspective definition that considers the interdependent nature of action of two or more individuals to produce a net payoff for all actors (Bshary and Bergmüller, 2008). Cooperation in this sense is an act that requires the coordination of two or more individuals to attain mutually beneficial outcomes. One goal is to distinguish intentional from incidental cooperation, wherein individuals converge on a mutually beneficial outcome as a consequence of following individual aims.

The simplest form of cooperation is by-product mutualism (or by-product beneficial behaviour; Bshary and Bergmüller, 2008) where independent self-serving actions lead to fitness benefits for both actors. The challenge for psychologists is to distinguish between intentional and incidental cooperation. For instance, prosocial actions have to be motivated for the benefit of recipients to be intentionally prosocial (Jensen, 2016a,b). This might seem intuitively obvious, but it is very difficult to demonstrate. Additionally, as opposed to competition which has been discussed in terms of cognitive abilities such as theory of mind, responses to stimuli and the nature of representation, cooperation research has primarily focused on individual motivations such as other-regarding concerns and social tolerance (Schmelz and Call, 2016). There is scope for a greater consideration of the cognitive underpinnings behind cooperation and understanding it will require a consideration of both motivations as well as the cognitive capabilities required, such as an understanding of the motivations and goals of others (perspective taking or theory of mind). An important area of investigation into coordinated action has been into joint intentions or shared goals, namely knowing the goals of others and being motivated to see those goals completed together (see, for example, Tomasello et al., 2005). To successfully coordinate their efforts, individuals will also need the ability to communicate these intentions to one another. In addition, individuals should also be able to inhibit immediate gratification, recognise the role of partners, suppress competitive tendencies, and potentially even weigh their own needs against that of the group as a whole, suggesting the need for strategizing capabilities, and the ability to perform approximate optimisation calculations. We have then a broad list of the capabilities that an animal may need to possess to successfully cooperate, and that we might expect them to employ when carrying out experimental cooperative tasks; theory of mind, maintenance of joint intentions, communication of intent, strategic calculation and inhibition of competition and aggression.

This last capability—inhibition of natural competitive urges—may be the most vital. Cooperation is one of the major benefits that might be afforded by group living (Silk, 2005; Sussman et al., 2005) but given competing individual interests it is challenging to understand how it is maintained, in part because the costs and benefits of group living are not equally distributed. Animals live in groups because it affords them adaptive benefits of sociality such as decreased predation (Foster and Treherne, 1981; van Schaik, 1983; Fichtel and Kappeler, 2002), increased foraging efficiency (Grueter et al., 2018) and mating opportunities for example (Majolo and

Huang, 2018). Larger groups may also provide more benefits than smaller ones, as they can better monopolise food sources (Janson and Van Schaik, 1988). For example, large groups of vervet monkeys are more likely to make incursions into the ranges of smaller groups than vice versa and to expand their ranges at the expense of smaller groups (Cheney and Seyfarth, 1987), larger resident groups of capuchin monkeys are more likely to win a between-group contest (Crofoot et al., 2008) and larger groups of gorillas have improved foraging efficiency compared to smaller ones (Grueter et al., 2018). Animals in groups may also spend less time looking for food, as they can pool and share information about its location and quality (Garber et al., 2009).

Foraging and moving in groups

While there are benefits to group foraging, there are costs associated with grouping, the foremost being within-group competition for resources (van Schaik, 1983). Animals in a group are in close proximity and share limited resources, particularly within the same food patches. Within-group competition for food may be as much as ten times greater than between-group (Janson, 1985, *Cebus apella*). Such competition may take the form of scramble competition, where individuals within groups similarly deplete resources, lessening the availability for all or contest competition, where aggressive interactions are used to gain access to food (Wrangham, 1980; Isbell, 1991). The outcome of these contests are dominance hierarchies that are based on relative size, strength, age or other factors.

Such dominance asymmetries may exacerbate the costs of group-living, particularly for those at the bottom of the hierarchy. Dominant individuals often obtain greater amounts or higher quality food than lower-ranking individuals when feeding at the same sites (Janson, 1985; Saito, 1996; White et al., 2007). Being a dominant individual is not advantageous in every circumstance, however, and the extent to which resources are unequally shared across ranks may depend on the particular dominance style of a species, which may be placed upon an axis with despotic at one extreme and egalitarian at the other (Thierry, 2000). The energetic and injury costs of maintaining dominance may be particularly intense in despotic species for example, and dominance may at times be a double-edged sword (see Sapolsky, 2005 for a review).

What is clear, however, is that the costs and benefits of sociality are often not equitably distributed, with some individuals claiming a greater share of resources than others, enjoying the benefits but little of the costs of group living. Conversely, lower-ranking individuals still participate in the work of group living (vigilance and predator defence) but may receive fewer benefits whilst incurring higher costs. The motivations and interests of individuals are also unlikely to always align. For example, the preferred time to move from one foraging patch to another may vary between individual group members due to divergence in activity budgets, dietary needs or simply to what extent they can monopolise feeding at a particular patch.

These inequalities lead to a tension between foraging in groups and foraging alone. If they wish to stay together, members of a group must often choose between mutually exclusive options (Conradt and Roper, 2005) with the result that synchronisation is likely to be more costly to some individuals than others, as it comes at the expense of their own nutrition (Conradt and Roper, 2000).

Of course, group-living animals do not always move together in synchrony. Animals may distribute themselves across patches within their territory to avoid feeding competition and maximise their individual fitness. The ideal free distribution (Fretwell, 1969) states that this distribution should be in proportion to the amount of resources available in each patch. A fission-fusion mode of group movement, as is seen in chimpanzees, spider monkeys and olive baboons (Symington, 1990; Chapman et al., 1995; Asensio et al., 2008; Alberts, 2013), may be the best way to maximise individual fitness in many contexts, particularly when there are differences in energy requirements amongst group members (Amici et al., 2008; Aureli et al., 2008; Sueur et al., 2011). Nevertheless, it remains true that group movement decisions can have important fitness consequences and an understanding of how consensus decisions are made is necessary. Decision-making may constitute a major cost of group living—in terms of time and energy. We know, for example, that in chacma baboons, making a decision about the direction of movement in the morning may take as much as 202 min, a loss of valuable foraging time (Stueckle and Zinner, 2008), and in chimpanzees, time to decide on a sleeping site (the interval between the first ‘nest grunt’ and nest building) can take an average of 30 min in a group as compared to 19 min alone (Janmaat et al., 2014).

Optimal decision-making in groups

Given the optimum decision for the group may differ from that of the individual, individuals cannot always make optimal decisions for themselves in a group context. There is increasing evidence that animal groups can come to collective decisions about when and where to move (King and Cowlishaw, 2009; King and Sueur, 2011; Strandburg-Peshkin et al., 2015; Janson, 2016). These decisions appear to be based on leadership (which is distinct from dominance) and quora or democratic consensus. However, what is less well understood is how they find the best solutions (Fischer and Zinner, 2011). In humans, consensus decisions range from the movement of crowds to complex international trade agreements. Indeed, many of the problems that people face result from either an inability to reach consensus, or from a breaking down of the decision-making process. An understanding of how decision-making works and why it may fail is therefore important (for reviews, see Couzin et al., 2005; Dyer et al., 2009; King and Sueur, 2011). What we do understand is the theoretical framework for optimal foraging at an individual level, have comprehensive evidence for the social and ecological challenges faced by group-living animals, and global-level models and empirical evidence for collective decisions. Although collective decisions are made at the group level, they are the outcome of individuals assessing how best to integrate their optimal decisions with the motivations and preferences of other individuals. The cognitive processes underpinning consensus and compromise and how collective decisions impact on an individual's ability to make optimal decisions within a social framework are virtually unknown.

We suggest that this deficit in our understanding of how groups make optimal decisions is due in part to a lack of concerted research into the cognitive processes underlying group behaviour. The behavioural ecology of primate groups has been thoroughly studied in terms of how social interactions, resource distribution and risks impact on individual fitness. Such studies have revealed the impact of group size on between- and within-group competition (Janson and Van Schaik, 1988), predation pressure (Sterck et al., 1997) and individual fitness and fecundity (Koenig, 2002; Majolo et al., 2008). The cognitive processes underlying these behaviours, however, have received less attention. Although the Social Brain Hypothesis, in particular, suggests that primate cognition has evolved to mitigate socioecological challenges, there is little evidence of, or a framework for studying, the cognitive mechanisms and processes needed to solve or mitigate social challenges (Dunbar and Shultz, 2022). In fact, despite references to 'social cognition', there is little real understanding of what this means or even an acknowledged consensus definition of 'cognition' within the study of animal social behaviour. One way to investigate these cognitive processes would be to investigate the impact of group size on group behaviour, specifically cooperation.

Within the primate literature group size has been investigated in relation to cooperation to an extent. King and Sueur (2011) discuss how vocal repertoires might facilitate and maintain cooperation in non-human primates as group size increases, and Samuni et al. (2021) find that the likelihood of an individual chimpanzee participating in an intergroup encounter increases with the number of other participants. Controlled experiments are lacking, however.

Working in groups

One field that has more explicitly studied group size in relation to group cooperation is human organisational psychology. Organisational or industrial psychology, as the study of behaviours in the human workplace, is by nature explicitly concerned with the interactions between individuals within a group—how they make consensus decisions, what is the ideal group size and composition for efficient collaboration and how conflicts of interest and intra-group aggression are overcome. Parallels can be drawn between this field and that of behavioural ecology, in that both focus on the benefits and costs of behaviour. Where they diverge is at what level these costs and benefits are assessed, with behavioural ecology focusing on individual fitness and organisational psychology the successful outcomes of the group (or company). There is a rich literature into human group dynamics in the workplace, exploring how group composition, size, and leadership can affect the efficiency and quality of decision-making (Gallupe et al., 1992; Laughlin et al., 2006). Primatologists studying human's closest living relatives may miss out by overlooking the human literature as these approaches can help us better understand group dynamics in the non-human 'workplace'.

Although the human office environment may seem far removed from the collaborative activities of other primates, there are parallels to be drawn. After all, both animals and humans are in the business of resource acquisition. Both may involve coordination, inhibition of competitive tendencies, strategic thinking and the navigation of social dilemmas to achieve optimal outcomes for everyone, suppressing free-riding tendencies.

The study of social behaviour in groups beyond the dyad utilising methods and theory rooted in human psychological research may allow us to ask questions such as, is there a threshold group size at which cooperation becomes unsustainable or too cognitively demanding for individuals due to difficulties in coordination, communication or motivation? What is the optimum sized group for mutually beneficial outcomes? What group composition achieves the best results? In this review we will look at how these questions have been answered in humans and consider what we might expect to find if they were similarly applied to non-human primates.

How are groups different from individuals?

Although groups are collections of individuals whose behaviour is expected to be a product of individual fitness maximisation, there are fundamental differences between groups and individuals. We should therefore expect the behaviour of an individual primate forager to be different when in a social context.

As well as affecting an individual's risk of predation and competition and their foraging efficiency, group membership is expected to affect their decision-making. Foraging primates need to make important decisions regarding where to forage and when and may also take part in coordinated group activities such as range defence, predator mobbing (Boinski et al., 2000) and hunting (Boesch, 1994). Being part of a social group complicates decision-making in numerous ways, as it involves keeping track of and synchronising with multiple individuals, as well as contending with differing opinions and interests. This has been explicitly examined in organisational psychology.

Insights from organisational psychology

The fundamental differences between groups and individuals, particularly with regard to decision-making, is a common topic within the field of organisational psychology, and the relative performance of group versus individual decisions has received a lot of attention. Jeffrey Rubin puts it succinctly: "two heads may be better than one, and occasionally worse than one, but they are always very different from one" (Rubin, 1984).

Early work into group performance demonstrated this, with the discovery that large groups of people may in some cases collectively outperform individual experts. This was found by Francis Galton in 1906 when he observed that a crowd could guess the weight of an ox with a surprising degree of accuracy, and more so than any one individual guess (Surowiecki, 2005). This phenomenon is known as 'the wisdom of crowds' and is thought to be more than a law of large numbers effect, as it is the diversity of opinions and heuristics that contributes to this 'collective intelligence' not simply the size of the crowd (Wagner and Vinaimont, 2010).

Groups may even be viewed as 'distributed systems' in which individuals have their own set of independent desires and perceptions yet still influence each other and interact to create emergent structures and properties that are not produced by any one individual. In this way people can contribute to collective behaviour patterns that they do not even perceive or understand. When cognition is seen not as an individual skill but simply as adaptive problem-solving, it is easy to see how collective group behaviours—in which information processing and computational capacity may be maximised as a consequence of its distribution across different but interacting 'units'—could be viewed as cognitive. This framework of 'group cognition', in essence, posits that systems larger than the individual are themselves cognitive (Gureckis and Goldstone, 2006; Goldstone et al., 2009; Theiner et al., 2010). For the purposes of decision-making in nonhuman primates however, we focus on individual behaviours in a group context, and how individual cognition is influenced by social interactions.

The effect of individuals in a group is very often not additive, and groups—particularly their collective and cooperative efforts—must be considered distinct entities, rather than just the combined effect of individual processes. We should expect this to be as true of primate group behaviours—including foraging and other coordinated activities—as it is of groups of humans. The question of whether groups outperform individuals is therefore a complex one. Within human group psychology, a few generalisations and observations have been made.

The first of these is that, although living in groups may be beneficial, there are instances in which individual efforts may suffer from being a part of a group. For example, groups can often inhibit the cooperative or prosocial actions of individual members. This is the case in the 'bystander effect', a phenomenon where people are less likely to intervene to help a victim when there are more other people present. This has even been found in online environments (Guazzini et al., 2019). The destructive effect of groups can also be seen in 'social loafing', the phenomenon of individuals exerting less effort when in a group than they would alone. The effect is thought to be motivational, with individual members feeling a lack of uniqueness and a sense that their efforts are less important (Rubin, 1984). This effect was first investigated by Ringlemann using tug-of-war experiments. The finding that as groups increase in size individual members become less productive is known as the Ringelmann effect (Ingham et al., 1974; Figure 1). In this way, individual-level cognitive processes can hamper group-level efficiency.

Group and individual decision-making may be measured and judged across numerous dimensions. These have included efficiency, accuracy, fairness, member satisfaction, leadership effectiveness and even rationality. Miner (1984) found that groups made more accurate decisions than that of the average individual, but equal to or inferior to that of the best individual ones. The decision-making strategy applied in this study also had a significant influence on relative group or individual performance. Vollrath et al. (1989) found groups to outperform individuals on memory tasks, having more accurate recall of facts, indicating that collective pooling and processing of information may outshine individual efforts, the 'pool of competence hypothesis.' Kugler et al. (2012) found that groups are (mostly) more rational decision-makers than individuals, due to increased prior experience, information sharing, processing capabilities, and monitoring.

Applications to primatology

From these observations—that group efforts are distinct from the additive efforts of individuals, and that many group properties may affect their performance—it is clear that groups (particularly their collective and cooperative activities) must be considered as a whole, rather than just as the combined effect of individual processes and behaviours. Such an understanding of group dynamics is however lacking when it comes to primate cognition. Phenomena such as social loafing and the Ringelmann effect for example would be interesting to investigate in primate cooperation experiments.

Although human group dynamics may seem removed from the activities of wild primates, parallels can be drawn. For example, we might expect to observe bystander effects in nonhuman

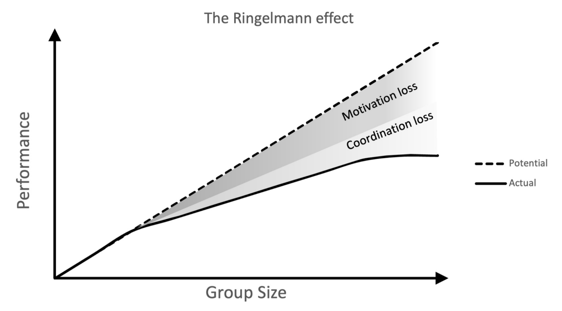

FIGURE 1
Visualization of the Ringelmann effect. As group size increases individual members become less productive. Actual performance is lower than potential performance, due to declines in coordination and motivation.

primates when it comes to group defence against predators, such as alarm calling or mobbing, or similar participatory deficits when it comes to extracting or catching food in a foraging context. Decision-making accuracy and efficiency in groups versus individuals are pertinent to movement decisions in foraging and selecting least-cost routes (Green et al., 2020). Pooling of knowledge may be important when individuals have differing knowledge of food or water locations during periods of scarcity (Rapaport and Brown, 2008; Garber et al., 2009). Thus, group dynamic phenomena shown in humans may also be relevant to non-human primates. Specifically, we might expect there to be significant influences of both the destructive and positive effects of group effort when it comes to making decisions about where to forage, when to move between resource patches, and which direction to move in.

How do groups move together?

The primary business of primates is foraging, and one of the most elementary forms of collective behaviour and decision-making process that can be studied regarding this is group movement. How then do primates, human and not, make these kinds of decisions (when to move, where next?) in the face of conflicts of interest, and keep a balance between the benefits of sociality and their own individual needs? Within the primate literature, these are questions that have only recently received much attention. Previously it was considered that very little was known about the mechanisms governing decision-making in vertebrate animal groups (Ward et al., 2008), as much of the research into the collective movement of groups has been conducted on insects (eusocial insects in particular) and birds.

What has been found in many cases in these taxa is that although collective behaviour can look very complicated, the underlying processes are often very simple. In many cases collective behaviour emerges through self-organisation; despite appearances, there is no “top-down” control, only local interactions giving rise to global patterns. Such self-organised systems have been described in migrating locusts (Bazazi et al., 2008) wherein the local interaction rule giving rise to their mass movement appears to be “move or be cannibalised” and starlings (Hemelrijk and Hildenbrandt, 2015) in which avoiding collisions with near neighbours results in extremely complex looking movement patterns. Such self-organisation can exist within very large animal groups, like locusts, where there is considered to be no individual recognition or dominance hierarchies, but it can also exist in smaller and more complex social groups, including humans and non-human primates. For example, Meunier et al. (2006) found through experimentation and modelling that collective movement in white-faced capuchins could be partially explained by anonymous mimetism—wherein individuals are more likely to mimic the actions of others, no matter who they are. In this way, their group movements simply depend on the number of individuals who have already moved.

Approaches used to understand group movement in insects have also been applied to human groups. For example, Shahhoseini and Sarvi (2017) directly compared ants and human pedestrians under an ‘emergency escape’ paradigm to investigate the rules governing their collective movement. Both humans and ants had to ‘escape’ a confined and crowded chamber that necessitated two streams of individuals merging into one. They found surprising similarities in the emergent collective movement patterns observed. In both, the rate of escape and efficiency of motion were in remarkable agreement and were similarly dependent on the architectural design of the environment. These results demonstrate how the same simple behavioural rules (in this case the forming and maintaining of separate, stable lanes of traffic) may govern collective movement in disparate species, and that these rules may work the same independently of species, cognitive abilities or group size.

Although such anonymous systems do exist, wherein movement decisions are a result of individual interactions, in both humans and other primates collective decisions are not always equally shared and often involve a form of leadership, whether intentional or automatic. In the emergency escape paradigm, for example, all the people possessed the same level of knowledge and received the same instructions, and thus a decision was not needed (Shahhoseini and Sarvi, 2017). Dyer et al. (2009) on the other hand experimentally tested how human crowds come to consensus decisions regarding direction of movement when only a small minority were informed about the target. They found that just a small number of informed individuals could successfully lead the naive ones to the target destination without any verbal communication or obvious signalling. Subtle cues appeared sufficient to initiate following behaviour. The presence of these informed individuals decreased both the time taken to reach the target and the degree of deviation from the target, emphasising the importance of informed leadership in collective decision-making.

Interestingly, when a conflict was introduced (informed individuals given one of two separate targets) the time taken to reach one of the targets as a group was not significantly increased. This indicates that in small groups humans are capable of resolving conflicts and come to consensus decisions fairly easily and quickly. The importance of the ‘tyranny of the majority’ or democratic forces was also evident, as in these conflict situations the direction that had the greatest number of ‘supporters’ tended to be chosen.

Similarly, in the last decade, the mechanisms behind group decision-making have started to be uncovered in wild non-human primate groups (King and Sueur, 2011). This review affirms that in many cases simple rules-of-thumb or heuristics are used to maintain group cohesion, rather than more complex tracking of individuals or use of signals. A review by Petit and Bon (2010) similarly emphasises that even in species deemed to have high cognitive complexity, simple self-organised processes can explain collective movement.

What is notable, however, is that the majority of this literature on group movement focuses on the ‘what’ and not the ‘why’. The models discussed (self-organisation and mimetism) focus on the physical and spatial mechanisms of movement, and high-level synchrony, and do not address the underlying individual cognition. They do not investigate why individuals are choosing directions for example, or what the quality of shared decisions might be to an individual. What is missing from the literature are studies that link such group-level behaviours to individual optimal foraging decisions, especially where there is social inequality. One review that does address the cognitive processes behind group movement decisions is Fischer and Zinner (2011), who emphasise the potential role of signals in eliciting motivational changes in group members, and thereby stimulating coordinated movement. A study by King and Cowlishaw (2009) also draws a link between individual variation in activity budgets and group-level behaviours. One of the few papers to explicitly evaluate the cognitive decisions underlying direction choice and patch preferences (Janson, 2016), shows that capuchin groups use information on time, energy and renewal rates to select patches. Finally, a recent paper proposes a framework to apply individual optimal foraging models to group-level decisions (Davis et al., 2022). This paper, although addressing the 'why' question and discussing how inter-individual differences influence collective decisions, does not address the psychology underlying individual decisions. There remains great potential for studies that explicitly investigate how individuals arrive at shared decisions.

Leaders and followers

What has been found repeatedly is that, like humans, social animals look to their group mates when making decisions, drawing information from the decisions others have made in order to make their own (King and Sueur, 2011). Individuals are more likely to choose options already chosen by others. Studying whose judgements they see as more valuable has revealed interesting dimensions of decision-making.

Within animal groups not all individuals are equal, and in particular, some are more informed than others. Leadership often emerges as a function of these information differences between individuals, and how successful leadership is likely to be depends on the importance individuals put on their own information versus that of others. How then are leaders chosen and why are they trusted?

In non-human primates

A quorum-like process to initiate and coordinate group movement has been observed in multiple primate species. In the collective movement of wild snub-nosed monkeys, adults were more likely to initiate decision-making with regard to initiation and direction, demonstrating how leadership may be based on age, experience, and/or dominance (Wang et al., 2020). However, in these monkeys, leadership did not fall on one particular individual, but rather several. Additionally, leaders were not despotic or omnipotent, and instead others 'voted' for them simply by copying the direction and movement initiated by the leader. This field study found that a threshold, or quorum level, number of voters was needed for successful collective decision-making. Similarly, Sueur et al. (2010) found that when Tonkean macaques made decisions on moving between patches of vegetation, the majority would 'vote' on several directions 'proposed' by several different initiators or 'leaders' by moving in that direction. This group decision can be viewed sequence of three different decisions, with three corresponding quorums, one to switch direction, one to choose the departure time, and one to choose the departure direction.

Another process that may be at work in these types of collective decisions is mimetism, a hypothesis that proposes an individual's probability of joining a movement increases with the number of individuals who have already joined the movement. This is distinct from quorum, in that there is no requirement for a specific threshold number. Mimetism may be selective, wherein relationships affect the process, or anonymous, where they do not. Wang et al. (2015) found that Tibetan macaques used a combination of mimetism and quorum thresholds to achieve collective movement, such that until a quorum level of adults (three) participated in a movement no group movement would occur. Once this level had been reached mimetism occurred—wherein the probability of any individual joining increased with the number that had already joined, but without a specific threshold number. Once a secondary quorum threshold was reached (seven) entire group movement always occurred.

Strandburg-Peshkin et al. (2015) also provide evidence for this shared and 'democratic' collective decision-making. By tracking wild baboons, they found that when deciding where to go individuals were more likely to follow multiple initiators who were in agreement. When agreement was low, an individual baboon was less likely to follow anyone at all, delaying the decision. When there was conflict over the direction of travel, the consensus achieved was dependent on the magnitude of difference in choices, such that when the angle between the two directional choices was large the group would choose one direction or the other, more often the one that had the most "supporters." When the angle was below a critical threshold the group instead compromised by moving in the average of the directions. This study demonstrates that primates may use multiple decision-making mechanisms (e.g., a quorum-based either/or decision versus an average) when engaging in collective movement, and also that the influence of high-ranking individuals can be limited, as dominance rank did not correlate with initiation success. Decisions were shared and based instead on majority preference. These results demonstrate the importance of social facilitation and the value of shared decision-making processes in some primate species. Instead of solely through despotism or a hierarchy of influence, consensus decisions in wild primates can emerge from shared processes. It is not necessarily an either/or situation however. Petit and Bon (2010) emphasise that decision-making in primates may be reached by a combination of different rules, both those based on inter-individual differences like dominance, and self-organised rules based on simple responses to local interactions.

In humans

The human literature has dived deeper into the dynamics of group decision-making and leadership. Within the human organisational psychology literature in particular, leaders and the attributes they possess is a large topic of study. Crucially, however, it must be noted that leadership can mean different things across disciplines, so parallels between leadership studies in humans and non-human primates can be difficult.

For example, leadership can be either automatic or intentional, passive or active. Within collective movements such as that discussed above, we can see that effective leadership can be given by even a small subset of informed individuals. As in self-organised systems, it can be based on simple rules for local interactions and can work without any explicit signals, or any group members knowing who the informed individuals are, the quality of their information, or even whether they are in the majority or minority. These informed individuals simply exert their influence through local interaction rules, and yet can thereby guide a whole group. For example, Dyer et al. (2009) found that when they asked a crowd of 200 people to walk around with just one rule "stay within an arm's length of each other" and no communication, only a handful of 'informed' individuals given a specific target were needed to move the whole naive group there. Similarly, in Sueur et al.'s (2010) Tonkean macaques, although initiators are described as leaders, their system of moving between patches may well conform to the main principles of self-organised group decision-making; individuals respond to local cues, and there is no explicit communication, no centralised processing of information and no centralised control. This type of passive leadership also emerges in human groups.

Conversely, leadership may also be conscious, intentional, and even striven for. Pulling apart these two types of leadership is not always easy, and it can be unprofitable to assume leadership conforms to the same principles cross-species. However, a look at the human organisational literature may highlight shared attributes of leadership, as well as reveal promising research approaches that may be applied to non-human primates.

The importance of social information (that gained through observation of or interaction with others) in human collective behaviour was demonstrated by Faria et al. (2010). This study found that pedestrians were more likely to cross a road if their neighbour had begun to cross. Interestingly this often seemed to lead to incorrect decisions (wherein pedestrians had to return to the curb to avoid a car), meaning that social information is sometimes misleading but may still be used even at the cost of individual safety, such is the influence of leader-follower behaviour in humans.

Leadership can arise from knowledgeable individuals (whether this knowledge is gained through age or experience, or simply heterogeneous access to information), but it can also emerge from other factors including dominance, sex, age, experience, as well as personality measures such as extraversion (Judge and Bono, 2000), ambition (Van Vugt, 2006) or a personal desire for authority (Fehr et al., 2013). These factors do not require that the leader be more knowledgeable. It can also arise as a consequence of heterogeneity of interests, due to physiological features (such as sex, age or reproductive status) that result in payoff differences. For example, an animal in oestrus may be hungrier and will therefore have a greater motivation to move to seek food, making them more likely to emerge as a leader (King et al., 2009). Thus, the ones in the greatest need may become the ones to lead, and this motivational component of leadership is thought to be present in humans just as other animals.

As discussed, leaders may also be either chosen and unwitting or self-appointed. For example, when people were given specific instructions about how to walk across a room whilst staying together in groups of four, contextual factors, like a person's location in the group, and individual factors, like characteristic locomotor behaviour, contributed significantly to the emergence of a leadership role. For example, participants in the front row (who could be directly observed by those in the back) more often became leaders (Lombardi et al., 2020). Interestingly, however, they also found that one specific individual tended to take on that role more than 60% of the time, initiating the directional change first and irrespective of where they were placed in the group. In doing so they took advantage of the collective movement and caused others to follow them, becoming a self-appointed leader. This study demonstrates how leader-follower behaviour can emerge out of a combination of simple geometric rules and individual differences, including personality.

Effective leadership may be particularly important when it comes to solving collective action problems. In small-scale societies in Bolivia, Ethiopia and South Sudan, effective leaders tended to have more capital than followers, be that age-related knowledge, body size or social connections. This abundance of capital is thought to facilitate leadership through mitigating some of the associated costs (Glowacki and von Rueden, 2015). This study also demonstrates the value of institutional leadership in resolving collective action problems, even in small-scale societies. The organisation of leadership around food production tended to be more *ad-hoc* and informal, whereas conflict resolution was more likely to involve an institutional leader—one that is formally recognised by the community. Formal leadership may be necessary in these situations as the costs of failure are potentially more destructive to the group than in a particular failure in a food production activity. In this way, leaders may facilitate the evolution and maintenance of cooperation, protecting cooperative societies and endeavours from the destructive effect of free riders, Cooperation has often been thought of as a Darwinian paradox, and one potential solution—punishment for non-cooperation—is often deemed to be costly to the punisher. However, the existence of a single leader who is willing to bear the costs associated with meting out punishment to free-riding individuals, in order to access the status, resources, and reproductive opportunities given to leaders may go some way to making sense of the paradox (King et al., 2009).

Such social norms and systems of enforcement and decision-making do however vary cross-culturally in small-scale societies. In the Batek hunter-gatherers of Malaysia, for example, foraging efficiency is successfully optimised through more egalitarian forms of decision-making, where movement decisions are not made by single individuals but instead through a process of informal group discussion involving most adults in the group (Venkataraman et al., 2017). Nevertheless, social norms and sanctions remain crucial in maintaining large-scale human cooperation (Fehr and Fischbacher, 2004; dos Santos et al., 2013) and, given this importance, could be another fruitful avenue of research in non-human primates. Large group cooperation experiments in controlled settings that give individuals the opportunity to exhibit enforcement strategies, such as punishment, could be very illuminating.

While group movement may be seen as the simplest form of collective behaviour there is evidence of more complex and potentially more cognitively demanding coordinated action in non-human primates. This includes goal-directed group behaviours such as group hunting, antipredator behaviour, and even joint tool use. Although more complex, where these behaviours overlap with movement decisions associated with foraging is that there is a similar need to employ negotiation and to overcome conflicts of interest, as well as to apply cognitive capabilities like joint intentionality, communication, and strategic calculation. Thus, it is helpful to consider both forms of cooperative behaviour when investigating the bounds of non-human of collaboration.

Coordinated action

In the wild

There are numerous examples of wild primates behaving cooperatively by working together to achieve mutually beneficial aims. Primate species can be placed along a spectrum of cooperativeness, from those that live a solitary lifestyle, only coming together to mate, to cooperative breeders at the extreme. In cooperatively breeding primates like the callitrichids, group members help to raise the young of the one breeding pair, at the expense of their own reproduction. The non-breeding helpers carry and provision the young with food, as well as engaging in joint resource and territory defence (Koenig and Rothe, 1991; Burkart and van Schaik, 2010). This form of cooperation is however rare in primates and such familial provisioning and defence may be viewed separately from coordinated, goal-directed behaviour. Behaviours such as territorial defence are found in non-cooperative breeders and goal-directed joint behaviour, such as joint tool use, may require different cognitive abilities than afforded by cooperative breeding and are not likely to be unique to animals like callitrichids (Thornton and McAuliffe, 2015; though see Burkart and van Schaik, 2016). In the context of tool use in particular, there is surprisingly little evidence of naturally occurring, coordinated, goal-directed behaviour in nonhuman primates. There are no observations of capuchin monkeys, for example, working together to crack nuts, with one supporting an anvil while another uses a hammer. There are no records of chimpanzees taking turns to elaborate upon a tool, like a stick for extracting ants. Although there is evidence of tool transfer in limited circumstances (from mothers to offspring), this does not constitute joint action, but rather sharing or helping at best (Musgrave et al., 2016).

However, joint action is not completely absent in nonhuman primates. As well as range defence and predator mobbing in many primate species (Boinski et al., 2000), coordinated action to achieve a shared goal has been seen with cooperative hunting (Boesch, 1994; Samuni et al., 2018) and intra and inter-group conflicts in chimpanzees (Mitani et al., 2010). Although coalitionary support in conflicts is more frequently seen in intra-group agonism (Nishida and Hosaka, 1996; Newton-Fisher, 2006; Smith et al., 2010), some of the most discussed examples of 'primate cooperation' come from observations of intergroup violence. Lethal intergroup violence in chimpanzees was first reported by Jane Goodall and has become known since as a prevalent feature of chimpanzee life (Goodall, 1986; Wrangham and Peterson, 1996). These conflicts have even been compared by some to human warfare, specifically that seen in nomadic hunter-gathers (Wrangham and Glowacki, 2012). Intergroup aggression in chimpanzees has been described as coalitionary in nature, with individuals working together, and relying on each other's support to minimise the risk of injury (Watts and Mitani, 2001).

Mitani et al. (2010) describe adult males participating in boundary patrols prior to intergroup aggression, in which they appear to move in a silent single file, attending to the signs of the others. Given that such patrols and attacks involve group effort, and entail bearing personal risks for the sake of group-level benefits, they might rightly be seen as evidence of purposeful cooperation. However, as Chalmeau and Gallo (1995) point out, using the existence of a common goal as the benchmark for cooperation may be misleading, as a mutually beneficial outcome may arise as a by-product of individually followed aims. Without evidence that joint goals are being conceived and maintained throughout it is hard to exclude the possibility that perceived cooperation is in fact the product of well-timed individual efforts. Willems et al. (2015) also report that communal range defence in primates rarely involves collective action in its strictest sense, in that it is instead best described as strategic individual-level decisions, without the need for jointly held aims.

Insights from experiments

Dyadic experimental studies have aimed to differentiate joint action from simultaneous individual actions, by ensuring that co-operators are interdependent. Such experiments have demonstrated the abilities of non-human primates to work together to solve food-acquisition problems. A powerful experimental paradigm for dyadic cooperation used in primates (as well as other taxa) is the cooperative pulling paradigm, notably the single-string paradigm (Melis et al., 2006b; Hirata and Fuwa, 2007). In this paradigm, two or more individuals work to pull food rewards towards themselves using an apparatus that one could not successfully operate alone. Experiments have consistently shown that nonhuman primates succeed at this (Jacobs and Osvath, 2015; Duguid and Melis, 2020). The task requires that pairs of individuals converge both spatially and temporally on a solution to a joint problem. It was first used by Crawford (1937) who had a pair of juvenile chimpanzees pull a heavy tray together. These individuals were trained to do so and received instructions from the experimenter on when to pull, calling into question the spontaneous nature of their cooperation (Tomasello and Call, 1997). Chalmeau (1994) expanded the methodology to an open-group design, allowing untrained individuals to spontaneously cooperate (or not). He found that one pair of individuals produced coordinated responses successfully solving the cooperative problem and retrieving food rewards, but that a dominant individual monopolised the apparatus, limiting the opportunities for successful collaboration. This paradigm was also used to demonstrate coordinated pulling in a pair of orangutans (*Pongo pygmaeus*) and group-housed tufted capuchins (*Cebus apella*) (Chalmeau et al., 1997a,b).

Cotton-top tamarins (*Saguinus oedipus*) were also found to successfully coordinate in this paradigm and appeared sensitive to the necessity of a partner (Cronin et al., 2005). However, they only did this after an extensive and multi-step training phase. Humans are known to coordinate spontaneously, thus studies that do not include such intensive training might be better comparisons to the nature of cooperative behaviour seen in humans. It may be that spontaneous cooperation is limited in non-human primates. For example, Hirata and Fuwa (2007) found that their chimpanzees only became successful at coordinated pulling after repeated trial and error. These observations, as with all laboratory-based experiments, do however come with the caveat that a lack of success in a controlled, lab-based task is not necessarily evidence of a complete lack of ability in a species. Lack of ecological validity is always an issue in such studies, just as lack of control raises questions about interpretations of field observations.

What controlled experiments have told us, in a clearer way than wild observations might, is that non-human primates do have some proficiency in purposeful joint action. They have allowed researchers to probe the cognitive mechanisms that might contribute to observations of joint action, in that monkeys and apes have been shown to coordinate their actions to achieve joint benefits. Studies into cooperative pulling, such as Chalmeau (1994) and Visalberghi et al. (2000), have demonstrated the ability of non-human primates to achieve joint goals—they are able to successfully act simultaneously to achieve a goal that is beneficial to both themselves and their partner. However, the cognitive underpinnings are still a matter of debate. In some cases, it was shown that the role of their partner was not fully understood (Chalmeau et al., 1997b; Visalberghi et al., 2000), and coordination was deemed to be incidental. Similarly, Petit et al. (1992) found in macaques that any seemingly coordinated action occurred likely by chance associations rather than purposeful synchrony or any recognition of roles. In other studies, however, the animals would wait for a partner before engaging in the task, indicating at least a rudimentary understanding of their role, and the interdependent nature of the task (Chalmeau et al., 1997a; Cronin et al., 2005; Melis et al., 2006b) and they would choose to work with the most effective partner (Melis et al., 2006a).

Cooperative pulling studies have also revealed potential motivational differences between humans and non-human primates in the context of cooperation. For example, using this paradigm Bullinger et al. (2011) and Rekers et al. (2011), demonstrated a collaborative bias in human children that is seemingly absent in chimpanzees, namely that children prefer to work together but chimpanzees do not, at least in contexts that could be argued to favour human subjects (Boesch, 2007). Experiments of this nature have demonstrated the motivational elements of cooperation; they also test for other cognitive abilities and limitations (Schmelz and Call, 2016). Chimpanzees, for example, do not appear to take the visual perspective of others in a task where they rely on a cooperative individual (Povinelli et al., 1996) yet they do appear to succeed in a competitive paradigm (Hare et al., 2000). Attempts to demonstrate false belief understanding (a component of theory of mind) in chimpanzees were unsuccessful (Call and Tomasello, 2008) until they were presented with a competitive scenario (Krupenye et al., 2016). Research and debate continue into how chimpanzees and other nonhuman primates coordinate, whether something like joint intentionality and perspective-taking are involved, as they appear to be in humans, or whether simpler cognitive solutions are used (Tomasello et al., 2005). Experiments continue to inform researchers of the role of cooperation and competition in the evolution of primate cognition (Hare and Tomasello, 2004).

Gaps in our knowledge

Despite their value, it is clear however that there is a limit to the usefulness of such experiments when it comes to thinking about the cognitive capacities required for large group collective behaviours in wild primates. Dyadic experiments are useful in showing us whether an individual is capable and sufficiently motivated to cooperate, as well as highlighting the cognitive mechanisms underlying these behaviours, however, they do not go very far in testing the limits of group-level cooperation. Cooperating with one other individual requires certain abilities (spatial and temporal coordination, social tolerance, motivation) but as the number of co-operators in a group increases we might expect these abilities to be stretched, and cooperation to become more challenging. In humans as groups increase in size individual members often become less productive in group tasks due to declines in both motivation and coordination (the Ringelmann effect; Ingham et al., 1974). However, this has not yet been tested in non-human primates, and so the effect of group size on cooperation in non-humans can only be speculated on.

For example, thus far, there is only one known study that experimentally tests cooperation in chimpanzees in groups larger than two (Suchak et al., 2014), wherein both duos and trios were tested in an apparatus-based food acquisition task. In this study successful coordination was achieved without training, success rates increased over time, and futile attempts (in the absence of a partner) decreased. The fact that groups larger than three have not been tested in a similar paradigm is surprising given that the most widely discussed instances of possible cooperation in wild chimpanzees, hunting and coalitionary attacks, involve the coordinated efforts of large groups. Thus, to further examine observational reports from the wild, and test whether and how chimpanzees and other primates are capable of coordinating as groups, there is a need for experimental studies beyond the dyad. Doing so will bridge the gap in our knowledge between ecological studies and lab-based cognition studies. The capabilities for joint action have been demonstrated but the limits have not been tested, and there are some very interesting questions yet to be answered. For example, are non-human primates able to enact and maintain coordinated action in large groups, or is there a threshold group size at which cooperation will break down and synchrony become unsustainable?

The relationship between group size and success in cooperative problem-solving has been more rigorously investigated in the avian literature. Morand-Ferron and Quinn (2011) examined the problem-solving performance of great and blue tits at automated devices and found that group innovation efficiency increased with flock size, validating a "pool of competence" hypothesis. Ashton et al. (2018) linked individual cognitive performance in magpies to group size, with those in large groups showing both increased performance in a "cognitive task battery" (measuring inhibitory control, associative learning, reversal learning, and spatial memory) and increased reproductive success. Perhaps most relevant to our questions is the finding that keas (*Nestor notabilis*) are capable of achieving cooperation in dyads, triads, and even tetrads in an experimental setting (Schwing et al., 2021). To our knowledge, this is the first such study that has tested instrumental cooperation in animal groups up to this size. A notable finding of this study was that success was dependent on the most dominant individual showing restraint and learning to stop monopolising the apparatus. An analogous 'beyond the dyad' cooperation study on non-human primates does not yet exist, and a clear deficit remains within our knowledge of primate group dynamics.

Such questions have been more fully addressed within the field of human organisational psychology, as described below. These studies have often focused on problem-solving tasks rather than large group collective decisions, yet, as with the kind of group coordination problems wild primates face, they often involve compromises between individual and group interests, as well as the pooling of differing inter-individual knowledge, and the generation and selection of solutions. Such studies have revealed that in humans group size may have strong effects on group productivity, efficiency, and accuracy of decision-making, as well as on individual effort, creativity and even free-riding.

Group size and composition effects on coordinated behaviours

As organisations and businesses are primarily concerned with optimising performance and efficiency, a common organisational question is "what is the optimal group size for group performance on a task." There are no straightforward answers, however. As discussed, the effect of individuals on groups is not always additive, thus the effects of increasing group size on performance can depend on a number of things, and the relationship is rarely linear. Group size is however expected to play a crucial role in group dynamics and outcomes. This is in part because increasing group size will increase the number of relationships and result in different interactions.

It might perhaps be expected that the larger the number of people in a group, the more likely it will be to succeed, due to increases in productivity. However, this may depend very much on the type of task. For example, Rubin (1984) makes a distinction between disjunctive and additive tasks. A disjunctive task, like a maths problem or a riddle, has only one correct answer and so all that is needed is for one group member to know it. Thus, the larger the group, the more likely you are to receive that answer. With additive tasks also, like a tug of war or a brainstorming session, where group members perform parallel functions, the effect of individuals is combined, and so large groups should outperform small ones. However, in tasks where there is no one correct answer or way of doing things (discretionary tasks), like the decisions made by juries, the relationship between group size and performance is much less clear.

Insights from organisational psychology

Group size effects

A number of 'tentative generalisations' have been made by organisational psychologists, and trade-offs identified (Rubin, 1984). For example, due to the fewer interactions and moving parts, smaller groups are considered to be more efficient. This efficiency may however come at the cost of decreased input and a lack of diverging, and often enriching, points of view. Larger groups may make higher quality decisions and may be more productive than smaller groups, generating more ideas or products, a point we expand on below. As an extreme example, population size plays a role in cumulative cultural evolution (Henrich, 2004; Derex and Mesoudi, 2020).

These questions have been studied experimentally, with varying outcomes. Some studies have found a positive effect of increased group size on performance. A study on electronic brainstorming, wherein groups interact *via* computers to generate and share ideas, found that larger groups generated more unique ideas and higher quality ideas than smaller ones (Gallupe et al., 1992), and a study on civilian scientists and technicians who were assigned to isolated U.S. Antarctic stations for one year found that perceived group compatibility and achievement was significantly lower at small stations than large ones (Doll and Gunderson, 1971). A study on supervisors and workgroups at a large manufacturing plant (Cummins and King, 1973) also found that group size was positively related to both productivity and leader-member relations in structured tasks. The authors suggest that a supervisor not being able to pay direct attention to all group members might be beneficial for production, so conversely too much oversight could inhibit group work.

An investigation on group size effects on problem-solving in US Airforce cadets also found positive effects of group work and group size (Holloman and Hendrick, 1971). Participants were randomly allocated to groups of differing sizes (between three and 15). In groups of all sizes, consensus decisions were more accurate than the averaged decisions of individual group members, validating the positive effect of social interaction on decision-making. Larger groups also made more accurate decisions than the smallest, although this effect seemed to stagnate after a certain group size, with the accuracy of groups of six not being significantly different from that of 12 or 15.

In a more recent study, this stagnating effect was found by Laughlin et al. (2006) who gave individuals and groups of two, three, four, or five two letters-to-numbers problems to solve. The groups performed better than the best efforts of the individuals, aside from the groups of two, who were equivalent to the best individuals. The groups larger than two did not differ from each other. Three was just as good as five, suggesting that a group of three is the best and most efficient size for this task.

These findings demonstrate that the relationship between group size and performance is not always linear (see Figure 2). Manners (1975) investigated the effect of group size on problem-solving effectiveness and consensus decision-making. He found that although the mean problem-solving performance of groups was significantly better than that of individuals, the results showed a quadratic relationship, such that there was an optimal group size, after which effectiveness began to decline. In this case, the size of groups varied between two and 18, and groups of 11 were the most effective. Interestingly, the relationship between group size and consensus making was hyperbolic, such that consensus dropped sharply with the addition of new members at first, but the effect lessened at larger group sizes. This was taken to mean that although smaller groups find it easier to reach an agreement than larger ones, in very large groups opportunities for changing the opinions of others are limited.

As predicted by social loafing theory (Ingham et al., 1974), group size can also have a negative effect on participation. Bass and Norton (1951) examined the effect of group size on member participation and leader emergence in initially leaderless groups. Average member participation declined as group size (between two and 12) increased, with groups of six found to be the most conducive to the emergence of leadership qualities. In a more recent study, social loafing was found to be more prevalent amongst members of larger subgroups working on an optimisation task (Meyer et al., 2016).

Other studies have found inhibiting effects of large groups on output. One such study by Bouchard and Hare (1970) investigated group size effects on brainstorming. Whether working in a group facilitates or inhibits creative thinking, innovation or problem-solving can be applied to animal groups as well as humans. This study measured the number of different solutions to a problem generated in groups of one, five, seven, and nine. They also compared 'real' groups in which individuals brainstormed together to 'nominal' groups composed of individuals who brainstormed alone and pooled efforts afterwards. They found that while overall the larger groups produced more ideas, the nominal groups were more effective than the real, indicating that the group-work approach inhibited idea generation. This perhaps unintuitive result suggests that in some cases pooled individual effort can be more productive than a group effort.

Group composition and inter-personal dimensions

As well as size, the structural characteristics of groups have also received attention. This includes spatial arrangement, as well as group make-up. Whereas the majority of the group size studies were done in the last century, the literature into group composition is relatively more modern, reflective in part of increased interest in the benefits of intra-group diversity. The decline in interest in group size dynamics (and group dynamics as a whole) is also thought to be symptomatic of a trend towards individualisation in workplaces (Schein, 2015).

Group diversity, in terms of gender, hierarchical status, and age is an aspect of group composition that has received particular attention. Choi (2007) investigated the impact of different demographic characteristics on creativity in employees of a Korean electronics company. They found that whilst differences in gender and hierarchical status decreased individual creativity, dissimilarities in age and performance level had the opposite effect suggesting that the effects of "diversity" as a concept cannot be generalised. Similarly, Wegge et al. (2008) found that age and gender had differential effects on group performance in federal tax offices. Age diversity correlated positively with group performance in groups solving complex decision-making tasks and increased gender diversity resulted in improved performance as compared to female-heavy teams. These effects of gender composition were most pronounced in large groups. As shown in the latter finding, group size and composition can interact. For example, Sidorenkov et al. (2018) found group size to be a moderator of inter-group conflict, such that increasing group size strengthened the influence of group characteristics, such as diversity and duration of membership, on conflict measures.

Finally, in addition to these composition factors, the interpersonal dimensions of groups have also been studied. Reddy and Byrnes (1972) found that groups that were more compatible in measures of control and affection (expressed and wanted) were

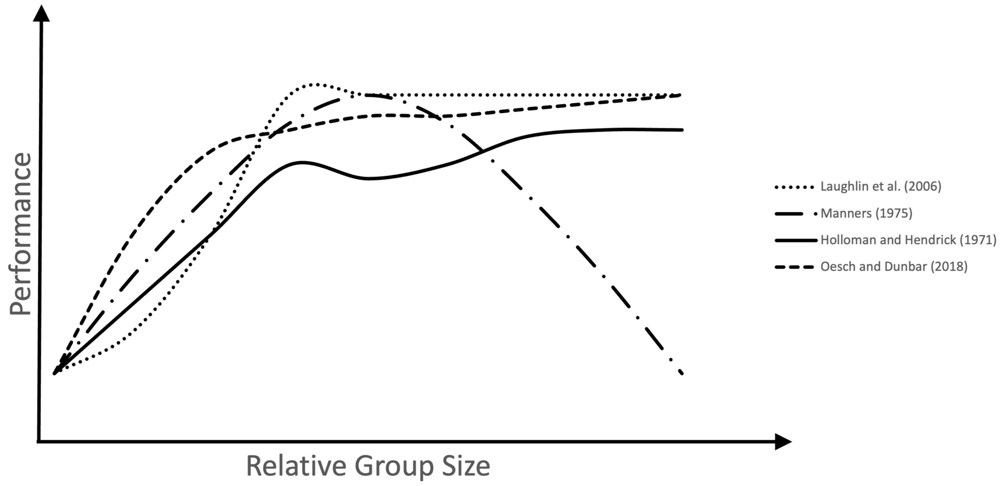

FIGURE 2
Group size effects on performance across several human studies. The measures of problem-solving performance used across these studies differed. These were, latency to solution (Laughlin et al., 2006), effectiveness (Manners, 1975), accuracy of decisions (Holloman and Hendrick, 1971), and foraging efficiency (Oesch and Dunbar, 2018). In all cases performance increases as small groups increase in size. However, in larger groups performance either decreases above an optimal size, or plateaus, with the benefit of more participants stagnating after a certain group size.

able to complete a decision-making and problem-solving exercise more rapidly than less compatible groups.

Future directions

Collective action problems

Collective action problems are not as well studied within non-human primates as they have been in humans. The importance of institutions and formal leadership in non-human primate social dilemmas may be a productive avenue of research for example. Overall, the human literature has thus far dived deeper into the dynamics of group decision-making. Given that we know considerable dominance and power asymmetries exist within primate groups, the question of how shared decision-making processes are maintained warrants further investigation.

The relationship between group size, group composition, and cooperation

Organisational psychology experiments have revealed important insights into the dynamics of groups that have parallels in primatology. The relationship between group size and its outputs (such as efficiency and productivity) is rarely linear, and the direction of this relationship depends on the type of task. Some findings have been less intuitive, such as that group work may inhibit individual productivity and idea generation, with pooled individual efforts having better outcomes. Many tasks have optimal group sizes, after which problem-solving accuracy and individual motivation to participate and cooperate begin to stagnate or even decline. If similar questions were put to non-human primate groups, we may well expect to discover similar effects at work. This becomes interesting when we consider the impact such effects would have on limiting the cooperative capabilities of primates in the wild, within behaviours like group hunting for example, and even on limiting the group sizes of cooperative primate species.

For example, by drawing inspiration from the human organisation literature, researchers could design experiments on non-human primate groups that ask;

A. How does group size affect the productivity, efficiency, and accuracy of cooperative efforts and what is the shape of this relationship?
B. How does task type (additive versus disjunctive) affect the direction of the relationship between group size and output?
C. How are outputs like consensus decision-making and idea generation (i.e. solutions to problems) affected by group size?
D. Is there an optimal group size for coordination tasks?
E. What effect does group size have on individual participation?
F. What effect does group size have on leadership emergence?
G. What are the interactions between group size and group composition factors, such as age and gender makeup? Do these factors have a greater influence on output in larger or smaller groups?
H. What is the impact of group size and composition on inter-personal factors? Does conflict increase or decrease in larger groups?

I. How does group composition, in terms of age, sex and status impact cooperation in groups?

By reference to both the behavioural ecology and human literature, tentative predictions can be made. We may find for example that with increasing group size problem-solving success becomes more likely, as the number of differently skilled individuals, the so-called "pool of competence," is increased. Conversely, we should also expect that as group size, and consequently, the number of interactions and relationships, is increased, group coordination, synchrony, and decision-making should become more challenging. This could be investigated through both wild and lab-based field studies in which groups of varying sizes are given extractive foraging problems that require group coordination (for example coordinated action and patch choice and movement tasks), and such effects could be evidenced by greater latencies to make decisions (i.e. when and how to act), more inaccurate or sub-optimal decisions, or a decrease in efficiency and productivity in tasks. A version of the Ringelmann effect would be expected, in which declines in individual motivation and coordination affect performance in cooperative tasks. We would also expect there to be an optimal group size for many tasks, which may well be larger than dyads that have so far been the focus of such experiments, but would also have an upper limit, after which performance declines. Effects like social loafing would be expected to be found in larger groups, wherein the individual motivation to participate and to take on a leadership role decreases with increasing group size, and often more sparsely distributed rewards. Finding such effects would tell us more about non-human primate cooperative motivations, as well as the strength of social norms and enforcement mechanisms in maintaining participation. Declines in coordination would also inform us about the limits of primate synchronisation abilities (joint action), as well as "we thinking" (joint intentionality). Results from such experimental group studies could then be used to make more informed predictions about what cooperative group behaviours we might expect to find in the wild and at what group sizes.

We would of course expect these socio-cognitive factors to work in concert with the ecological ones discussed, both mediating group size in natural groups. For example, the size of a group may be limited by factors such as the challenges of coordination, as well as the pressures of between-group competition.

Discussion

There are parallels to be drawn between the very different fields of behavioural ecology and human organisational psychology. In both group-level behaviours are studied and limits discussed and in both cognition is often assumed or implied. Organisational psychology, like behavioural ecology, typically does not consider the cognitive processes underlying behaviour but instead focuses just on the behaviour itself. Comparative psychologists on the other hand rely on experiments to infer the cognition of individuals but are often guilty of considering the effects of individual mental processes on behaviour at the expense of all else, including real-world social and ecological pressures. There then exists a need for an integration of behavioural ecology and comparative psychology, to better understand the relationships between behaviour and selective pressures.

In this review, we have identified an arena for such integration, that of group collaborative behaviours in non-human primates. Currently what we know about the cognition of groups comes from dyads, and what we know of group dynamics comes from large wild groups. This knowledge deficit should be filled by experimental studies on groups of varying size which explicitly investigate the cognition underlying joint action, leadership roles, optimisation problems and motivation.

What our brief review of the primate cooperation literature has shown is that experimental work is based on just a few experimental paradigms, primarily string-pulling, which, although useful in demonstrating certain abilities, have limited ecological validity, especially given dyadic cooperation is not the norm. Rather, instead of problem-solving, what wild primates do is make large-group collective decisions—about where to go and when—many times a day. Gaps in our knowledge of what properties of groups might influence these processes, and how they are maintained in the face of conflicts of interest persist. There appears therefore to be a need for an expansion of more naturalistic experimental studies which investigate more relevant behaviours, including patch foraging and group hunting. We suggest that controlled experiments in a wild setting on natural groups might be the best way to investigate these behaviours, as it would combine ecological validity with scientific rigour, as well as allow the opportunity to study groups whose size has not been directly dictated by human intervention. Such an approach has been used by Van de Waal et al. (2014) for example, to study social learning in vervet monkeys. However, although controlled experiments in a natural setting would be the best-case scenario, the proposed questions could also be investigated in captive settings. Although often artificial size and composition, groups in zoos have frequent variation in size, both within zoos and between due to transfers, and offer the practical and scientific benefits of a more easily controlled environment. Cowl et al. (2020) for example, investigated how crested macaques responded to disturbances of the group composition when a zoo manipulated the group size. Naturalistic foraging tasks have also been conducted in zoo settings, such as Ozturk et al. (2021) who investigated food-finding in mandrills. Additionally, in order to satisfactorily investigate group size effects, particularly in the wild where group size is less easily manipulated, it would also be necessary to compare many different groups. This would require a large collaborative effort, but initiatives such as Many Primates (Primates et al., 2019), which was founded to facilitate collaboration across numerous study sites in primate cognition research, can serve as a model.

A review of the human organisational literature has given us potential research questions and approaches, as well as indications of what such studies might find. This includes a non-linear relationship between group size and performance indicators, such that for some collaborative tasks optimal group sizes should exist, beyond which cognitive capacity and motivation become stretched. When translated to group behaviours in the wild, such as making coordinated movement decisions when foraging, and engaging in group hunts, such findings could be very revealing.

Drawing inspiration from the human literature and investigating the effects of group size and composition on group performance may help to bridge the gaps that we have identified between what is known about groups and individuals, allowing us to gain a better understanding of how non-human primates navigate the challenges of sociality.

Author contributions

LW: writing—original draft preparation, conceptualization, and data curation. SS: supervision, writing—review and editing, and conceptualization. KJ: supervision, writing—review and editing, conceptualization, and data curation. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Development of embodied capital: Diet composition, foraging skills, and botanical knowledge of forager children in the Congo Basin

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The embodied capital theory states that the extended juvenile period has enabled human foragers to acquire the complex foraging skills and knowledge needed to obtain food. Yet we lack detailed data on how forager children develop these skills and knowledge. Here, we examine the seasonal diet composition, foraging behavior, and botanical knowledge of Mbendjele BaYaka forager children in the Republic of the Congo. Our data, acquired through long-term observations involving full-day focal follows, show a high level of seasonal fluctuation in diet and foraging activities of BaYaka children, in response to the seasonal availability of their food sources. BaYaka children foraged more than half of the time independent from adults, predominantly collecting and eating fruits, tubers, and seeds. For these most-consumed food types, we found an early onset of specialization of foraging skills in children, similar to the gendered division in foraging in adults. Specifically, children were more likely to eat fruit and seed species when there were more boys and men in the group, and girls were more likely than boys to collect tuber species. In a botanical knowledge test, children were more accurate at identifying plant food species with increasing age, and they used fruits and trunks for species identification, more so than using leaves and barks. These results show how the foraging activities of BaYaka children may facilitate the acquisition of foraging skills and botanical knowledge and provide insights into the development of embodied capital. Additionally, BaYaka children consumed agricultural foods more than forest foods, probably reflecting BaYaka's transition into a horticultural lifestyle. This change in diet composition may have significant consequences for the cognitive development of BaYaka children.

KEYWORDS

botanical knowledge, cognitive development, embodied capital theory, forager diet, juvenile foraging, Mbendjele BaYaka subsistence, sedentarization, sugar content

Introduction

The subsistence strategies and diet of human foragers are characterized by feeding on high-quality and difficult-to-acquire foods (Kaplan et al., 2000) such as meat (Milton, 1999), tubers (Laden and Wrangham, 2005), and honey (Crittenden, 2011). The embodied capital theory states that the extended juvenile period has enabled humans to acquire a wide variety of foraging skills to collect these foods and that this dietary shift has resulted in increased brain capacities (Kaplan et al., 2000). Referring to skills and knowledge as embodied capital, Kaplan et al. (2000, 2003) compared these processes of development with investments in stocks. They posit that the investment of learning extensive foraging strategies has coevolved with the large brain size, elongated childhood, and dietary shift in our species (Kaplan et al., 2003). In addition to hunted (e.g., animals) and extracted foods (e.g., tubers and honey), human foragers gather above-ground foods from wild plants, such as fruits and leaves. Even though fruits can be collected more easily regarding extraction costs, trees with ripe fruits are often sparsely distributed in space and time (Milton, 1993; Janmaat et al., 2016). The overall energetic costs of gathering have been found to exceed those of hunting and fishing (Gallois and Henry, 2021). Still, most studies on forager subsistence strategies have not considered fruit foraging and botanical knowledge, rather focusing on the importance of meat and tubers in the human diet (e.g., Jones and Marlowe, 2002; Walker et al., 2002; Tucker and Young, 2005; Gurven et al., 2006; Demps et al., 2012; Schniter et al., 2015). Moreover, previous studies on forager subsistence strategies have focused on adults, resulting in limited knowledge on the foraging contributions of children and how they acquire foraging skills and knowledge (Hewlett, 2017; but see Lew-Levy et al., 2017).

Here, we examined the seasonal diet composition, foraging behavior, and botanical knowledge of children in a contemporary forager society, the Mbendjele BaYaka (henceforth: BaYaka), in the Republic of the Congo. BaYaka children were observed to forage independently from a young age (Lew-Levy et al., 2020b), probably because foods of the BaYaka are distributed close to camp and the environment is considered relatively safe (Lewis, 2002), contrasting the ecology of other foraging societies (Blurton Jones et al., 1994; Draper, 2013). BaYaka start learning nut-cracking skills from early childhood, but their efficiency reaches maximum only later in adulthood (Boesch et al., 2019), suggesting that the children need a substantial learning period to acquire complex foraging skills (Lew-Levy et al., 2021). To understand children's foraging and learning strategies for different types of food sources, it is important that foraging behaviors are observed throughout the year to account for seasonal changes in the types and abundance of available foods (Bahuchet, 1988; Kitanishi, 1995). In this study, we first investigated the diet composition and foraging activities of BaYaka children, while focusing on the seasonal variation and the ratio between forest and agricultural foods. Second, we examined what factors influence their collecting and eating probability of fruit/seed and tuber species, which are the most-consumed food types of the BaYaka children in our study community. Third, we examined the BaYaka children's botanical knowledge of foraged plant species and which plant parts they used for species identification, by conducting tests with pictures of 12 different plant species.

In the Congo Basin the availability of different foods changes seasonally and annually (Bahuchet, 1988; Kitanishi, 1995), with a high availability of fruits and seeds in the wet season, a brief period of caterpillar abundance during the late wet season, and honey collecting and fishing during the dry season (Bahuchet, 1988; Hladik and Bahuchet, 1994; Kitanishi, 1995). Tubers are mainly collected during the dry season, even though their phenology is poorly known (Bahuchet, 1988). Meats are available in all seasons, although animal densities have likely declined over the years due to deforestation and high demands for bush meat. In addition to forest foods, the diet of the BaYaka include agricultural foods. They obtain these from a complex relationship with Bantu-speaking farmers on the edges of the forest (Bahuchet and Guillaume, 1982; Joiris, 2003; Takeuchi, 2005), in which agricultural foods are exchanged for labor and forest products (Kitanishi, 1994, 2003). In the studied community, the BaYaka also cultivate their own crops, including oil palm fruits (*Elaeis guineensis*), cassava (*Manihot esculenta*), papayas (*Carica papaya*), plantains (*Musa* × *paradisiaca*), taro (*Colocasia esculenta*), and sweet potatoes (*Ipomoea batatas*; Bombjaková, 2018).

Based on the seasonal variations in the availability of forest foods (Bahuchet, 1988; Kitanishi, 1995), we expected that BaYaka children's diet composition and foraging activities will also fluctuate periodically. Seasonal foods such as caterpillars, honey, forest fruits, and seeds were expected to only be eaten for short periods, while less seasonal foods such as animals, fish, and leaves might be more consistently eaten throughout the year. When available, fruits were expected to be eaten frequently, as they are often sugar-rich and children in many societies prefer sweet foods (Desor and Beauchamp, 1987; Pellegrino et al., 2018). This preference for sweet foods, which is lower in adults, has been linked to physical growth during childhood (Coldwell et al., 2009). Additionally, fruits are generally less protected from consumption compared to other food types, such as leaves, mushrooms (e.g., chemical defenses), and seeds (e.g., hard shells that require access to iron or stone tools; see *Panda oleosa* in Boesch et al. (2019)). Besides fruits, we expected that children predominantly consume tubers, based on their importance in forager societies in the Congo Basin (Kitanishi, 1995; Sato et al., 2012). Finally, we expected meat to make up a substantial part of the diet as well, as was observed by Kitanishi (1995). Compared to Kitanishi (1995), who collected data in the same region as our study more than two decades ago (Supplementary Figure S1), we did expect to find higher percentages of agricultural foods in BaYaka children's contemporary diet. The rapid deforestation over recent decades has likely caused a decrease in the availability of forest foods, potentially increasing their dependence on agricultural foods.

Based on the embodied capital theory (Kaplan et al., 2000) and previous research on gender-segregated children groups (Lew-Levy and Boyette, 2018; Jang et al., 2019b; Lew-Levy et al., 2020a) we expected children to learn and acquire foraging-related knowledge and skills from an early age and that this is related to a gendered division of foraging activities in adults. BaYaka men mainly hunt for animals and climb trees for fruits, seeds, and honey, whereas women spend more time collecting fish and plant foods such as tubers (Lewis, 2002). We propose that such a gendered division in foraging activities likely coincides with a division in specialized foraging skills, enabling the human species to have a much broader diet than our closest living relatives, the non-human great apes. Yet the question whether this gendered division in foraging activities is already present in childhood remains poorly understood. Hence, we also investigated whether boys and girls forage for different food items, and thus acquire distinctive foraging-related skills and knowledge. We specifically expected that the age and gender of the children and their foraging group composition will predict which foods will be collected. We expected that boys will primarily forage for fruits/seeds and girls for other plant foods such as tubers, based on the gendered division observed in adults (Lewis, 2002). However, as the BaYaka share the majority of food items within the community (Lewis, 2014), we expected that the age and gender would not specifically predict the food types and species consumed by children. We also expected that the BaYaka children are more likely to collect and consume fruits with higher sweetness levels as they have shown a strong preference for sweet foods (Kandza, 2018), like children in other societies (Desor and Beauchamp, 1987; Pellegrino et al., 2018).

Lastly, in the botanical knowledge test of foraging-related plant species, we expected boys to outperform girls as boys are expected to climb trees to collect fruits, seeds, and honey, and that older children are more accurate at identifying plant species than younger ones, as predicted by the embodied capital theory and age-structured knowledge (Kaplan et al., 2000; Lew-Levy et al., 2021). Furthermore, we expected that the children will identify the plant species mostly by using the fruit/seed part, as this is the part eaten and often brought back to camp to be shared. Children may use tree trunks as well for identification. Being able to identify a species by its trunk can enable foragers to detect potential trees from further distances and provides opportunities for inspection and fruit discovery (see Janmaat et al., 2013a). Children can also use leaves for species identification in their search, especially when inspecting the canopy or areas with fallen leaves.

Methods

Children and region

We conducted our study with a total of 27 BaYaka children ($N_{\text{girls}} = 14$, $N_{\text{boys}} = 13$), who volunteered to participate. The children lived with their community in a logging concession close to the *Motaba* river and the village *Djoube*, in the northern part of the Republic of the Congo (Supplementary Figure S1). Besides 'BaYaka,' the study community are often referred to as 'Mbendjele,' 'Baaka,' 'Baka,' or 'Aka' (Kitanishi, 1995; Köhler and Lewis, 2002; Bombjaková, 2018; Jang et al., 2019a). The children who participated in this study were estimated to be on average 9.7 years old (range: 4.5–17.1). Due to the absence of birth records kept by the BaYaka, the ages were estimated based on information about birth order provided by the family. Additionally, BaYaka or Bantu of whom the exact age was known were used as anchor points. Using these anchor points, the ages of other BaYaka were estimated based on an inter-birth span of 2.5 years, following Hill and Hurtado (2017).

During our data collection period, the BaYaka community resided in camp *Mbaso* from March to August 2016, camp *Bongo* from November 2019 to January 2020, and in camp *Kuona* from February to March 2020 (Supplementary Figure S1). The environment around the village *Djoube* has been described as Congolian Lowland Forests (Loubelo Madiela, 2018; Jang and Boyette, 2021), often with clear signs of logging activity. This logging activity causes rapid deforestation in those areas where the BaYaka are residing (Lewis and Nelson, 2006; Laporte et al., 2007). At each camp site, rainfall and temperature data were recorded daily over multiple fieldwork periods from 2015 to 2020. As expected from the seasonality described by Hewlett (1991), the proportion of rainy days per month was lower from November until February than from March until September, having a peak in August (Supplementary Figure S2). The temperature was relatively constant throughout the year (Supplementary Figure S2).

Observational data collection

The focal children were accompanied on foraging trips during a rainy period of 6 months in 2016 (March – August; by V.K.) and during a dry period of 5 months in 2019–2020 (November – March; by J.V.), with most children being observed over multiple days (Supplementary Tables S1, S2). Observational data were collected using continuous focal sampling (Martin and Bateson, 2007), recorded by a combination of a GPS (Garmin 64S), that created location and time stamps, and a voice recorder (Jang et al., 2019a). The observation period for each child was split across two consecutive days to lower the potential effect of the long-term continuous presence of the researcher. In general, these 2 days were characterized as follows: the first day started with a picture test in a tent, after which observational data were collected from the moment the focal child left camp on a foraging trip until the end of the last meal of the day back in camp. On the second day, data were collected from sunrise until the first time the child would arrive back in camp after the start time of observations on the first day. This way, a full day of observation was ensured for each child. During observations, data were recorded on foraging (e.g., inspecting, digging), eating (e.g., food name, food type), and group composition (e.g., number of boys and girls). We defined inspection as moving one's head in combination with a fixed gaze, either in the direction of the canopy or the ground (Janmaat et al., 2013b).

In total, the 27 children were observed for approximately 798 h, separated over 114 days covering every month of the year except for September and October. Since children were observed on two consecutive days, we analyzed these 114 days as 57 full-day observations (Supplementary Tables S1, S2). To visualize the variation in the diet composition and foraging activities throughout the year, the study period was divided into five periods (Supplementary Table S1). The focal child was asked to participate after a random selection depending on whether the child was present in the camp, in most cases alternating between girls and boys to account for seasonal variation in food availability. Informed consent was obtained from both the child and their parent(s)/caretaker(s) after the data collection method had been explained in their language.

Diet composition and foraging activities

Using the long-term observational data, we examined seasonal variation in diet composition and foraging activities of BaYaka children. Each food item was categorized into different food types including fruit, tuber, seed, leaf, honey, aquatic animal, caterpillar, and terrestrial animal (Supplementary Table S3). The food item was assigned as a fruit when the children ate the fleshy pulp that is often rich in sugars, whereas it was assigned as a seed when they ate the lipid-rich parts. Food items were furthermore distinguished between forest and agricultural foods (Supplementary Table S3). Similar to other dietary studies (see Lim et al., 2021), the time spent eating a certain food item was used as an indication of its percentage in the diet. This way, the behavior could be observed without interference by weighing each food item, which likely would have affected the children's behavior such as eating and sharing. When a combination of multiple food items was eaten in a cooked dish (e.g., fish with *Gnetum* leaves), the total eating time was divided by the number of different food items eaten, assuming equal eating time on each food item. Foraging time was estimated based on the food items that were searched for and collected during foraging trips outside the camp, either in the forest or in gardens. Trips and behaviors unrelated to foraging were excluded from the calculation, including visiting other villages or camps, washing, swimming, collecting firewood, playing, dancing, cooking, and gardening. To estimate the total foraging time, it was assumed that a child would forage for a particular type of food (e.g., tubers) until they started looking for or collecting another food type (e.g., fruits). If it was not clear, the child was asked what they were looking for. Finally, travel time back to camp was not considered to be part of the foraging time when no food items were collected during travel.

Nutritional analyses

Botanical identifications of food plants were performed at the Herbarium of the Institut de Recherche en Sciences Exactes et Naturelles (IRSEN) in Brazzaville, after which the dried samples were transported to the German Centre for Integrative Biodiversity Research (iDiv) to determine nutritional content. Samples were dried by storing them in small ziplock bags with silica. For the sugar extraction, 100 ± 5 mg of ground sample material was mixed with 1 mL of 70% methanol, vortexed and boiled for 5 min in a water bath (GFL, Burgwedel, Deutschland) at 90°C. Subsequently, samples were transferred to an ultrasonication bath (Thermo Fisher Scientific, Dreieich, Germany) for 15 min. Solid material was separated from the supernatant *via* centrifugation for 10 min at 14,000 × *g* in a benchtop centrifuge (Thermo Fisher Scientific, Dreieich, Germany) at room temperature. These supernatants were transferred to new reaction tubes (Eppendorf, Hamburg, Deutschland) and pellets were extracted a second time with 1 mL of 70% methanol and a 15 min ultrasonication step. After centrifugation, the supernatants were combined and the evaporation loss of methanol was compensated by bringing extracts to the predetermined average weight of Eppendorf tubes containing 2 mL of 70% methanol. Each sample material was extracted three times and samples were stored at −20°C until analysis. Extracted samples were measured with a high-performance anion-exchange chromatography system ICS-5000 with a pulse-amperometric detector (Thermo Fisher Scientific, Dreieich, Germany) for carbohydrate analysis. As mobile phase, eluents (12 mM and 150 mM NaOH) were manually prepared from 50% (w/w) NaOH (FisherChemical). A gradient program was used at a flow rate of 0.2 $\mathrm{mL\,min^{-1}}$ (Supplementary Table S4). As stationary phase a CarboPac-column (Dionex CarboPac, PA210-4 µm, 2 × 30 mm, Thermo Fisher Scientific, Dreieich, Germany) was used. The detection was performed *via* an electrochemical detector with a disposable Au-electrode and a quadrupole pulse- waveform at a sampling rate of 2 Hz. For carbohydrate quantification calibration curves were measured for D-(+)-glucose, sucrose, and D-(−)-fructose (10 Carbohydrate Kit, SigmaAldrich) in a range of 1–10 $\mathrm{mg\,L^{-1}}$. The samples were diluted accordingly to be detectable within the ranges of the calibration curves. The quantification was undertaken with the Software Chromeleon (Version 7.2.6). Standard and samples were injected with a volume of 2.5 µL. The sample compartment was cooled to 20°C and the column compartment heated to 30°C.

To determine sugar richness, the concentrations of glucose, fructose, and sucrose were summed (Supplementary Table S5). Subsequently, total sweetness was calculated based on the sweet perception in Aka foragers (Hladik et al., 1986) by multiplying these concentrations with 1.00, 6.55, and 7.76, respectively, and then taking the sum over the three sugar types (Supplementary Table S5).

Collecting and eating probability of fruit/seed and tuber species

After examining the seasonal variation in diet composition and foraging activities, we focused on the behavior while foraging for fruits, seeds, and tubers. As these were the most-consumed food types, we examined the factors influencing their collecting and eating probabilities. For some of the food items, availability was difficult to assess by independent ecological surveys. Hence, to determine the availability of each food species throughout the year, we supplemented our dataset with data collected similarly and simultaneously on foraging women (see Jang et al., 2019 for wet season). Based on all these data, a specific food species that was foraged and/or eaten on a specific date was assumed to be available the week before and after that date. This way, for each child a list of food species was created that could have potentially been collected and eaten. These available food species were the sample units of our models. Subsequently, the observational data of each child were used to determine for each food species whether it was collected and/or eaten or not. We analyzed the collecting and eating behavior as a binary response to circumvent potential issues with temporal autocorrelation (e.g., a child might be more likely to find more tubers after finding the first one of a particular species) and to minimize interobserver differences.

Picture test of foraging-related plant species

During the dry season of 2019–2020, we tested the botanical knowledge of the 18 children ($N_{\text{girls}} = 8$, $N_{\text{boys}} = 10$) for whom behavioral data were collected (Supplementary Table S2). We selected 12 plant species that produce edible fruits or seeds known to be eaten by the BaYaka (Supplementary Table S6), then tested the ability of the children to correctly name these plant species. Providing the pictures of the plant parts had the advantages of testing the different parts separately and disentangling the possibility that children would have remembered individual tree species based on spatial knowledge from previous foraging experiences. For each of the 12 plant species, we located multiple individuals of which pictures were taken from the fruit/seed, leaf, trunk, and bark (Supplementary Figure S3). Most pictures of the fruits/seeds were taken previously during the wet season. The pictures of the trunk were taken at breast height, from a distance that made the base of the trunk visible (Supplementary Figure S3D). For the bark, the pictures were taken from a short distance including a rectangular incision in the tree ensuring that both the inner and outer bark were visible (Supplementary Figure S3E), similar to pictures provided in botanical books (Hawthorne and Jongkind, 2006). The children were all used to seeing 2D-pictures from previous research in 2013, and each year between 2015 and 2018. Nonetheless, to test for potential effects of 2D-pictures, we also included the actual leaves. These leaves were dried to simulate the leaves they would encounter in the leaf fall area surrounding the trees. Five different samples were used for each picture of the part of a certain plant species and its dried leaves. Subsequently, we randomly selected which sample was demonstrated on a laptop to a child and in which order. In total, all 60 combinations of plant parts and plant species were shown to each child: 12 species with for each species a picture of one of the four parts (i.e., fruit/seed, leaf, trunk, bark) and the actual leaf. One child with albinism was tested, but these data were excluded from the analysis since her eyesight limited her ability to interpret the pictures.

Since it was previously found that foraging-related plant knowledge is widely shared among camp members (Salali et al., 2016), we investigated whether there was an indication the children shared the answers of the botanical test with each other. To prevent this, the order and samples demonstrated were randomized and the children were not told which answers were correct. If they somehow would have figured out which 12 plant species were included in the test, we predicted that they would answer one of the names of these 12 plant species more frequently when they did not know the correct answer (i.e., guessing), which could have led to children tested later scoring higher on the test.

Testing gendered division in foraging behavior

To examine the differences in foraging-related behaviors between boys and girls, we performed Mann–Whitney *U* tests. Based on the gendered division in adults we expected boys to spend more time foraging for fruits, seeds, caterpillars, and honey, and girls to spend more time foraging for fish and tubers. This might require different types of foraging behaviors since the boys are expected to forage for food items often located in the canopy while the girls are expected to forage on items found on the ground. Therefore, we expected boys to inspect the canopy more often and climb more trees. In contrast, girls were expected to inspect the ground more often and to collect larger quantities of tubers.

Model F_{col} and F_{eat}: Fruit/seed species collecting and eating probability

To examine the effects on the collecting and eating probabilities of fruit and seed species, we constructed two Generalized Linear Mixed Models (GLMMs; Baayen et al., 2008), using a binomial error structure with logit link function (models F_{col} and F_{eat}; Supplementary Table S7). The response variable consisted of the collecting (model F_{col}) and eating (model F_{eat}) probability (1 or 0) of all fruit and seed species that were expected to be available on the day of observation. As fixed effects, we included age, gender, weighted average number of boys and men in the group, sweetness, food habitat, and food type. The observation time per day varied (mean = 14.00 ± 2.05 h, range: 11.44–20.12), mostly depending on the moment the child would eat the last meal on the first day and would arrive back in camp on the second day. Therefore, observation time was log-transformed and included as an offset term. The random effects were observation day, child, and food species. For both models, we initially included all possible random slopes and their interactions to control type I error rate (Schielzeth and Forstmeier, 2009), creating a Maximal Model (Barr et al., 2013). These models included the random slopes of sweetness, habitat, and food type within observation day; of age, number of boys and men, sweetness, habitat, and food type within child; and of age, gender, and number of boys and men within food species. The models were subsequently simplified by the removal of the unidentifiable correlations between the random slopes of sweetness, habitat, and food type and their intercept observation day (Matuschek et al., 2017). For both models, we tested for multicollinearity by calculating the Variance Inflation Factors (VIFs) for the fixed effects in the models (Zuur et al., 2010). With a maximum VIF of 1.910, there was no indication of multicollinearity. Based on the stability analyses, the fixed effects of habitat and food type were slightly unstable for the F_{col} model, as well as habitat in the F_{eat} model. The direction of the effect of food type in F_{col} and habitat in F_{eat} was, however, stable. In total, 364 fruit/seed collecting and eating probabilities were included in each model, based on 57 observation days in which 27 children were observed with a total of 15 different species (species availability: mean = 6.39 ± 2.63, range: 1–10). We expected that older children are better at climbing trees and thus have a higher probability of collecting fruit and seed species compared to younger children. Especially boys were expected to focus more on this type of foraging. However, if the fruits and seeds are subsequently brought back to camp, we expected everyone to have an equal probability of eating the food by demand-sharing. In addition to the age and gender of the focal child, we also expected the number of boys and men in the group to have an effect if there is a gendered division in foraging activities. Groups with more boys and men were expected to spend more time on fruit/seed-related foraging trips and to have a higher probability of finding these food items. We expected children not yet able to climb trees to be dependent on older children to collect the fruits and seeds if they are high in the canopy. For this, the weighted average number of boys and men during trips outside of camp was calculated. To calculate this, we took into account the duration of each observed behavior and the according group composition. Finally, we expected the characteristics of the fruit/seed itself (i.e., sweetness, habitat, type) to influence the collecting and eating probability. Agricultural fruits and seeds were thought to have a less complex spatio-temporal distribution and to have some nutritional advantages over forest fruits, increasing the probability of collecting and eating them. As mentioned, we expected sweeter food items to be preferred. We therefore expected that the children prefer to collect and eat fruits over seeds.

Model T_{col} and T_{eat}: Tuber species collecting and eating probability

For the collecting and eating probabilities of the tuber species, two GLMMs (Baayen et al., 2008) with binomial error structure and logit link function were constructed (models T_{col} and T_{eat}; Supplementary Table S7). In these models, the response variable consisted of all available tuber species for each child and whether they were collected/eaten or not (1 or 0). The fixed effects were age, gender, weighted average number of girls and women in the group, and habitat. Observation time (log-transformed) was again included as an offset term. The same random effects (i.e., observation day, child, food species) were included as in models F_{col} and F_{eat}. The created Maximal Models (Barr et al., 2013) had the random slope of habitat within observation day; of age, number of girls and women, and habitat within child; and of age, gender, and number of girls and women within food species. Subsequently, all the correlations between the random slopes and intercepts were removed to deal with convergence issues (Matuschek et al., 2017). The maximum VIF found for these models was 1.557, showing no indication of multicollinearity. Model stability analyses showed that the fixed effects were unstable for model T_{col}, similar to habitat in model T_{eat}. However, the direction of the effect of gender in T_{col} and of habitat in T_{eat} was found to be stable. The sample size in each model consisted of 250 collecting and eating probabilities of tuber species, using data from 57 observation days in which 27 children were observed with eight tuber species (species availability: mean: 4.39 ± 1.63, range: 2–8). We expected that older children are better at collecting tubers than the younger ones, but that the tubers will subsequently be shared and eaten by all children in the camp. Since tuber collecting is considered women's work (Lewis, 2002), we expected that girls would have a higher probability to collect the tuber species than boys. In contrast to the fruit/seed models, we hypothesized that instead of the number of boys and men, here the weighted average number of girls and women in the group to have a positive effect on the collecting probability. As in the fruit/seed model, we also expected agricultural tubers to have a higher probability of being collected and eaten than forest ones because of their easier localization and higher nutrition, but also because of lower digging costs.

Model B_{know}: Botanical knowledge of foraging-related plant species

To examine the effect of age, gender, and plant part shown on the botanical identifications, we constructed a GLMM (Baayen et al., 2008), using a binomial error structure with logit link function (model B_{know}; Supplementary Table S7). The probability of correctly identifying the plant species was used as a response variable, being either 1 or 0. The fixed effects of the model were age, gender, and the part of plants shown to the children, and as random effects, we included the sample, child, and plant species. After initially creating a Maximal Model following Barr et al. (2013), including the random slopes and their interactions with the intercepts (Schielzeth and Forstmeier, 2009), the model was simplified. In the Maximal Model we included random slopes of part shown within child; of age, gender, and part shown within plant species; and of age and gender within sample. The correlation between the random slope of gender and sample was unidentifiable and thus removed (Matuschek et al., 2017). All model assumptions were checked, including collinearity. With a maximum VIF value of 1.227 there was no indication of multicollinearity. Model stability analyses demonstrated that the fixed effects were stable. In total, 1,020 questions were asked to the 17 children consisting of four pictures (i.e., fruit, leaf, trunk, bark) and a dried leaf from 12 different foraging-related plant species. We expected that the children's botanical knowledge linearly increases with age during childhood and that boys are better at identifying foraging-related plant species than girls are. The children are expected to be best at identifying the fruit/seed itself, followed by the trunk, leaf, and bark. If there is no effect of 2D-picture, equal scores are expected between the pictures of leaves and the actual leaves.

Implementation

All statistical analyses were performed in R (version 1.1.419; Rstudio Team, 2016). For the GLMMs (Supplementary Table S7) we used the function *glmer* of the package *lme4* (version 1.1-23; Bates et al., 2015). To increase the probability the model would converge, the optimizer *bobyqa* was used. The VIFs were calculated using the *vif* function in the *car* package (Fox and Weisberg, 2019). The functions *glmm.model.stab*, *ranef.diagn.plot*, and *boot.glmm.pred* were provided by dr. R. Mundry to assess model stability, to test the assumption that the Best Linear Unbiased Predictors (BLUPs; see Baayen et al., 2008) were normally distributed, and to calculate the bootstrapped 95% confidence intervals (using 1,000 bootstraps), respectively. Finally, effect sizes (Nakagawa et al., 2017) were calculated with the *r.squaredGLMM* function from the package *MuMIn* (version 1.43.17; Barton, 2020), with the marginal R^2 reporting the effect size of the fixed effects and the conditional R^2 reporting the effect size of fixed and random effects. All categorical fixed effects were manually dummy coded and centered, and all covariates were z-transformed to increase the likelihood that the models would converge and to make the estimates comparable. To test the overall effect of each model, likelihood ratio tests (LRTs) were used (Dobson, 2002), comparing the full model with the null model using the *anova* function. These null models consisted of the offset term and the random effect structure, lacking all fixed effects (Forstmeier and Schielzeth, 2011). For the individual effects, LRTs were used with the *drop1* function, comparing all possible models lacking one of the terms (Barr et al., 2013; Harrison et al., 2018).

Results

Dietary composition and foraging activities

Out of the 798 h of observational data, 89 h were spent eating (11.2%) and 218 h were spent foraging (27.3%). More than half of the time the children foraged independently from the adults (52.4%), primarily in peer groups. Children spent on average most time eating fruits (39.6%), followed by tubers (29.1%), seeds (15.4%), leaves (4.3%), caterpillars (3.8%), aquatic animals (2.4%), honey (2.3%), and terrestrial animals (1.4%), with the remaining food items (e.g., mushrooms, insects other than caterpillars, or market foods only available in the village) making up 1.6% (Figure 1; Supplementary Table S3). Figure 1 shows that they spent most time foraging for tubers (40.5%), followed by fruits (16.2%), aquatic animals (15.8%), caterpillars (9.3%), honey (8.4%), seeds (5.1%), leaves (2.0%), terrestrial animals (1.8%), and others (1.1%).

The eating and foraging of these different food types varied across observation periods (Figure 1). With the exception of leaves and terrestrial animals, the food types show clear seasonal differences in eating and foraging time (Figure 1). Caterpillars, for example, were exclusively foraged and eaten during period III (Figure 1), which corresponds with the late wet season (Supplementary Figure S2). Foraging and feeding on honey had a clear peak during period V (Figure 1), the late dry season (Supplementary Figure S2). Furthermore, aquatic animals were also not consistently foraged throughout the year, being absent in periods III (late wet season) and IV (early dry season). Even though children were not observed to forage for aquatic animals during period IV, they did eat them. The foraging and feeding on seeds largely correspond with the wet season (period I to III; Figure 1). The seasonal variation in fruit foraging and eating becomes clear when focusing on the proportion of forest and agricultural fruits, with forest fruits exclusively being foraged and eaten during the wet season (period I to III; Supplementary Table S8).

Of the total eating time of the children, 42.8% concerned forest foods, compared to 55.5% agricultural foods and 1.7% food of other or unknown origin (Supplementary Table S3). The majority of the eating time on tubers consisted of agricultural species, with the exception of period IV, in which 83.2% of the eating time on tubers was on forest tubers (Supplementary Table S8). This was largely due to one species, *Dioscoreophyllum cumminsii*, which accounted for 96.9% of the time spent eating forest tubers (Supplementary Table S8). Even though forest tubers were eaten less than agricultural ones, more time was spent foraging for those forest tubers than for agricultural tubers (Supplementary Table S8). It furthermore took, on average, five times as long digging to find a forest tuber than an agricultural one during the dry season (302.03 ± 206.07 s and 57.79 ± 39.90 s, respectively).

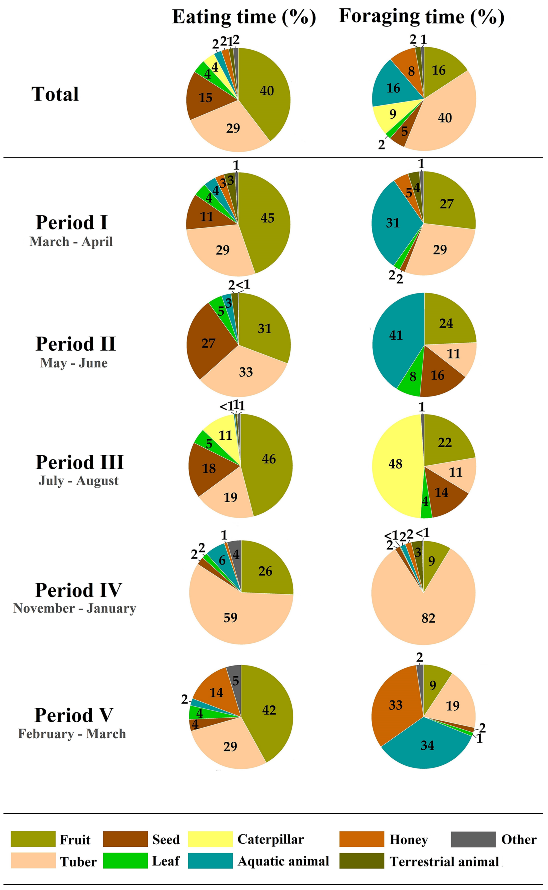

FIGURE 1
Diet composition and foraging activity. Shown are the percentages of time eating and foraging for different food types over the year. The periods visualize the fluctuation throughout the year. Period I to III corresponds with the wet season of 2016 and period IV and V with the dry season of 2019–2020.

The eating time and diet composition of boys and girls were highly similar, except for honey which was almost absent in the diet of girls (Figure 2). Boys spent a slightly lower proportion of the day foraging than girls (boys: 23.4%; girls: 31.6%), spending more time in camp (49.7 and 48.9%) and on trips unrelated to foraging (26.8 and 19.4%), such as washing or playing (see Methods; Figure 2). There were, however, larger differences between the foraging activities, with boys spending more time foraging for fruits (18.4%), honey (18.0%), and seeds (8.6%) than girls (13.7, 0.7, 2.2%, respectively; Figure 2). Girls, on the other hand, spent more time foraging for tubers (50.4%) and aquatic animals (20.4%) than did boys (28.1 and 10.9%, respectively, Figure 2).

It was found that during foraging trips the canopy was scanned and inspected more often per hour by boys ($N_{\text{boys}} = 13$, $\text{median}_{\text{boys}} = 2.542$) than by girls ($N_{\text{girls}} = 14$, $\text{median}_{\text{girls}} = 0.257$, $U = 14$, $p < 0.001$). Additionally, boys spent a higher proportion of their foraging time climbing trees than did girls ($\text{median}_{\text{boys}} = 0.030$, $\text{median}_{\text{girls}} = 0.000$, $U = 42$, $p = 0.002$). In contrast, girls tended to scan, inspect, and check – either with hand or machete – the ground more frequently per hour foraging ($\text{median}_{\text{boys}} = 0.447$, $\text{median}_{\text{girls}} = 1.206$, $U = 129.5$, $p = 0.065$) and collected significantly more tubers per hour foraging ($\text{median}_{\text{boys}} = 0.000$, $\text{median}_{\text{girls}} = 0.204$, $U = 132.5$, $p = 0.041$) than did boys. Finally, girls spent a higher proportion of their foraging time digging compared to boys ($\text{median}_{\text{boys}} = 0.251$, $\text{median}_{\text{girls}} = 9.932$, $U = 140$, $p = 0.018$).

Model F_{col} and F_{eat}: Fruit collecting and eating model

Contrary to our predictions, we did not find an effect of age, gender, number of boys and men or of any of the fruit/seed characteristics (i.e., sweetness, habitat, type) on the probability of fruit/seed species being collected (F_{col}: Full-null model comparison: $\chi^2 = 5.766$, df = 6, $p = 0.450$; Table 1). However, for the eating probability, there was an overall effect of these factors (F_{eat}: Full-null model comparison: $\chi^2 = 14.791$, df = 6, $p = 0.022$). It was found that fruit/seed species had a higher probability of being eaten when there were more boys and men in the group ($\chi^2 = 4.049$, df = 1, $p = 0.044$; Table 1). Furthermore, agricultural species were more likely to be eaten than forest species ($\chi^2 = 7.991$, df = 1, $p = 0.005$; Table 1).

Model T_{col} and T_{eat}: Tuber collecting and eating model

For the tuber species collecting model, a significant overall effect was found of age, gender, number of girls and women in the group, and habitat on the probability of being collected (T_{col}: Full-null model comparison: $\chi^2 = 12.100$, df = 4, $p = 0.017$). Specifically, girls were more likely to collect tuber species compared to boys ($\chi^2 = 9.276$, df = 1, $p = 0.002$; Table 2). For the eating probability, none of the factors were found to have an effect (T_{eat}: Full-null model comparison: $\chi^2 = 5.052$, df = 4, $p = 0.282$).

Model B_{know}: Botanical knowledge foraging-related plant species

Finally, we found an overall effect of age, gender, and plant part shown on the probability of correctly identifying the foraging-related plant species (B_{know}: Full-null model comparison: $\chi^2 = 28.284$, df = 6, $p < 0.001$). There was a positive effect of age ($\chi^2 = 12.712$, df = 1, $p < 0.001$; Table 3; Figure 3) and an effect of plant part shown on the probability of correctly identifying the foraging-related plant species ($\chi^2 = 9.885$, df = 4, $p = 0.042$; Table 3; Figure 4). Specifically, the children were more likely to correctly identify the plant species based on a picture of the fruit/seed compared to a picture of the leaf (Estimate = 2.052, SE = 0.900, $p = 0.023$) or a picture of the bark (Estimate = 2.735, SE = 0.883, $p = 0.002$; Table 3; Figure 4). A picture of the trunk also had a higher probability of being correctly identified than a picture of the bark (Estimate = 1.556, SE = 0.573, $p = 0.007$; Table 3; Figure 4). In addition, children scored better on the leaf itself than on a picture of the bark (Estimate = 1.044, SE = 0.486, $p = 0.032$; Table 3; Figure 4). We found no statistical difference between the pictures of the leaves and the actual leaves themselves (Estimate = −0.358, SE = 0.368, $p = 0.330$; Figure 4), suggesting that the 2D-demonstration mode (i.e., the picture) did not have an effect. Spearman's rank correlations indicated that the children had not learned the plant species names in the botanical picture test before they performed the test, as we found no significant correlation between the test number and the proportion of the 12 species incorrectly identified ($\rho = -0.346$, $p = 0.160$, $N = 17$). As expected from this, the children did not score higher with the end of the testing period approaching ($\rho = -0.054$, $p = 0.832$, $N = 17$).

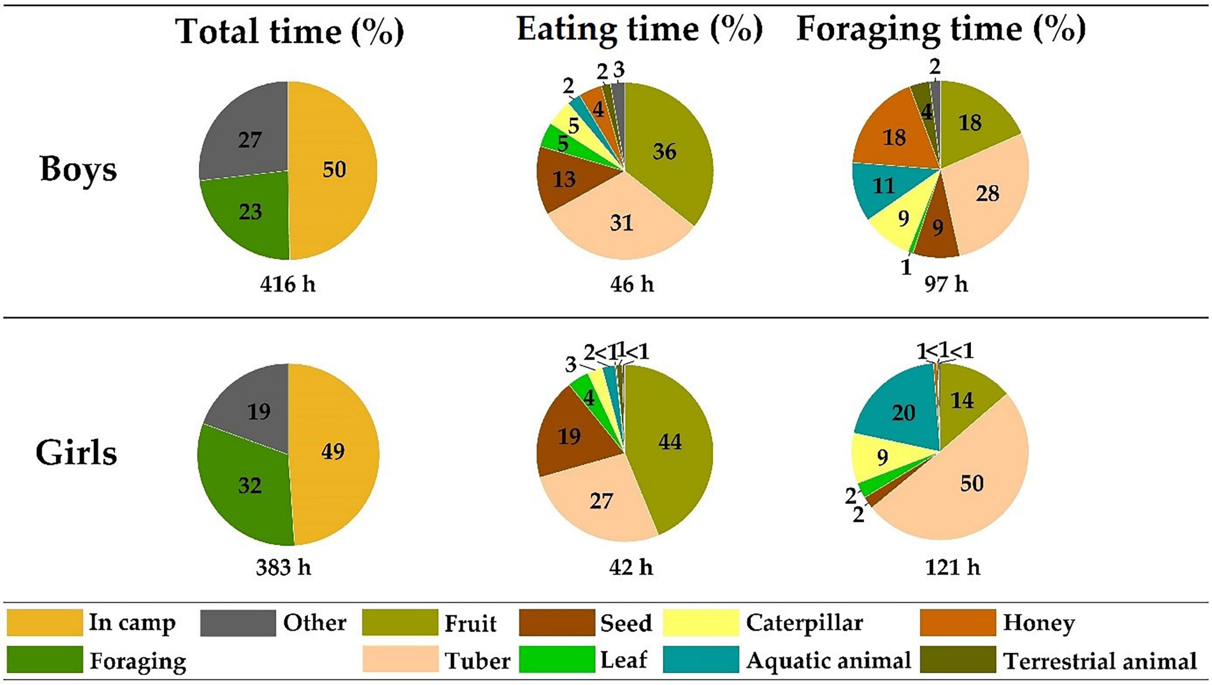

FIGURE 2
Differences in diet composition and foraging activities between boys and girls. Indicated is the difference in eating and foraging time on the food types between boys (N=13, median age=10.2, range: 4.5–16.5; observation time: 416h, eating time: 46h, foraging time: 97h) and girls (N=14, median age=9.1, range: 5.5–17.1, observation time: 383h, eating time: 42h, foraging time: 121h). The pie charts on the left indicate the percentage of time spent in camp, on foraging trips, and on trips unrelated to foraging. The middle and right pie charts indicate the percentage of time spent eating and foraging, respectively, on the different food types. For the definition and calculation of eating and foraging time, see Methods.

Discussion

Our results indicate the presence of a gender-specific early onset of the development of foraging skills and an age-related development of botanical knowledge in contemporary forager children, providing insight into the development of embodied capital. The BaYaka children spent most of their foraging time independent from adults, primarily eating and foraging on fruits, tubers, and seeds across seasons (Figure 1; Supplementary Table S3). Other food types, such as caterpillars and honey, were also widely eaten and foraged, but were more seasonally restricted (Figure 1; Supplementary Table S3). We also found a gendered division in the food types that were foraged (Figure 2). With more than half of their diet consisting of agricultural food, the children had a mixed-subsistence diet (Supplementary Table S3). Focusing on the fruit and seed species, children had a higher probability of eating the agricultural species (Table 1). A larger number of boys and men in the group increased the eating probability of fruit and seed species (Table 1). In addition, tuber species were more likely to be collected by girls (Table 2). Finally, the botanical knowledge of the children improved with increasing age (Table 3; Figure 3). The children were most likely to identify the foraging-related plant species based on its fruit/seed, followed by its trunk, leaf, and bark (Table 3; Figure 4).

Diet composition and foraging activities: Seasonal fluctuations and mixed-subsistence

The consistently high percentages of fruits and tubers in the diet of the BaYaka children is likely explained by a combination of preference and availability. In total, 17 different fruit species were observed being eaten, of which the agricultural oil palm fruit, papaya, and plantain were available during nearly the complete study period. For the tubers, eight species were eaten, of which both the agricultural species (i.e., cassava, taro, and sweet potato) and the forest ones, including *D. cumminsii* and *Dioscorea* spp., were seasonally widely available during the study period.

During period IV the agricultural tubers were rarely foraged and eaten, which is likely due to where the BaYaka resided during this period (i.e., camp *Bongo*). This camp is characterized by its fishing traps and numerous forest tuber patches, with no gardens nearby. Children were not observed to forage for aquatic animals during this period, even though they did eat fish. This is probably because the adults emptied the fish traps, compared to other fishing types such as dam-fishing in which children actively participate (Jang and Boyette, 2021). Hardly any fish were foraged and/or eaten during the peak of the wet season in period III, likely due to high levels of water making dam-fishing impossible. During this wet season, the children instead foraged for the highly seasonal caterpillars and seeds. Honey, another highly seasonal food item, was mainly foraged during the late dry season.

Our findings on diet composition are largely in line with previous research on the seasonal variation in diet and foraging activities of the Congo Basin foragers (e.g., Bahuchet, 1988; Kitanishi, 1995). As expected, forest fruits, seeds, caterpillars, and honey were highly seasonal, while terrestrial animals, fish, leaves, and tubers were more consistently collected and consumed throughout the year. These seasonal changes in dietary composition emphasize the importance of long-term data collection when focusing on subsistence strategies and the diet composition of human foragers. In addition, the high proportions of fruits and tubers were as expected based on previous research. Children

TABLE 1 Probability of collecting and eating fruit and seed species.

Term	Estimate	SE	$\mathrm{CI}_{\mathrm{lower}}$	$\mathrm{CI}_{\mathrm{upper}}$	χ^2	df	P	Min	Max
Model $\mathrm{F}_{\mathrm{col}}$	Effect on collecting probability fruit/seed species								
Intercept	−4.478	0.587	−23.989	−3.675	–	–	–	−4.797	−4.077
Age[a]	0.000	0.268	−1.020	0.873	0.000	1	1.000	−0.158	0.076
Gender[b]	−0.182	0.633	−2.798	2.022	0.083	1	0.773	−0.629	0.368
Nr of boys and men[a]	0.511	0.360	−0.261	3.183	2.105	1	0.147	0.273	0.839
Sweetness[a]	0.207	0.271	−0.899	1.806	0.562	1	0.454	−0.003	0.338
Habitat[b]	−0.089	0.778	−2.707	2.430	0.013	1	0.909	−1.793	0.992
Food type[b]	−0.849	0.699	−6.645	0.489	1.433	1	0.231	−1.599	−0.459
Model $\mathrm{F}_{\mathrm{eat}}$	Effect on eating probability fruit/seed species								
Intercept	−3.587	0.485	−5.101	−2.797	–	–	–	−3.830	−3.354
Age[a]	−0.245	0.255	−0.891	0.265	0.886	1	0.347	−0.353	−0.142
Gender[b]	−0.213	0.453	−1.229	0.778	0.212	1	0.645	−0.519	0.054
Nr of boys and men[a]	**0.416**	**0.204**	**−0.012**	**0.951**	**4.049**	**1**	**0.044**	**0.294**	**0.578**
Sweetness[a]	−0.228	0.220	−0.986	0.225	1.021	1	0.312	−0.457	−0.078
Habitat[b]	**1.855**	**0.626**	**0.790**	**3.764**	**7.991**	**1**	**0.005**	**1.004**	**2.256**
Food type[b]	0.350	0.597	−0.891	1.862	0.345	1	0.557	0.018	0.604

It was analyzed whether the probability that a fruit or seed species was collected ($N = 364$; model $\mathrm{F}_{\mathrm{col}}$) or eaten ($N = 364$; model $\mathrm{F}_{\mathrm{eat}}$) was influenced by the age and gender of the children, the number of boys and men in the group, or by the sweetness, habitat (forest/agriculture), or type (fruit/seed) of the fruit/seed species. The estimates are shown together with the standard errors (SE), lower and upper 95% confidence interval ($\mathrm{CI}_{\mathrm{lower}}$ and $\mathrm{CI}_{\mathrm{upper}}$), likelihood ratio tests results (χ^2, df, p-value), and the minimum and maximum estimates based on the model stability analyses (min and max). Significant results ($p < 0.05$) are indicated in bold. Model $\mathrm{F}_{\mathrm{col}}$: Full-null model comparison: $\chi^2 = 5.836$, df = 6, $p = 0.442$; marginal R^2: 0.037, conditional R^2: 0.181. Model $\mathrm{F}_{\mathrm{eat}}$: Full-null model comparison: $\chi^2 = 14.791$, df = 6, $p = 0.022$; marginal R^2: 0.159, conditional R^2: 0.325. [a] Z-transformed; mean ± SD of original variables age, number of boys and men, and sweetness were 9.737 ± 3.321, 2.788 ± 1.924, and 156.137 ± 158.820, respectively. [b] The variables gender, habitat, and food type were dummy coded with girl, forest, and fruit as reference, respectively.

TABLE 2 Probability of collecting and eating tuber species.

Term	Estimate	SE	$\mathrm{CI}_{\mathrm{lower}}$	$\mathrm{CI}_{\mathrm{upper}}$	χ^2	df	P	Min	Max
Model $\mathrm{T}_{\mathrm{col}}$	Effect on collecting probability tuber species								
Intercept	−4.409	0.706	−48.803	−3.300	–	–	–	−66.576	−4.076
Age[a]	0.309	0.367	−0.866	3.084	0.651	1	0.420	−7.335	0.561
Gender[b]	**−2.184**	**0.775**	**−11.872**	**−0.454**	**9.276**	**1**	**0.002**	**−11.312**	**−0.647**
Nr of girls and women[a]	0.099	0.313	−2.195	1.415	0.101	1	0.750	−5.277	0.316
Habitat[b]	0.118	0.823	−3.818	3.848	0.021	1	0.885	−0.165	34.641
Model $\mathrm{T}_{\mathrm{eat}}$	Effect on eating probability of tuber species								
Intercept	−4.307	0.611	−5.899	−3.183	–	–	–	−5.208	−4.144
Age[a]	−0.101	0.161	−0.457	0.247	0.385	1	0.535	−0.324	0.005
Gender[b]	0.351	0.389	−0.495	1.256	0.797	1	0.372	0.118	0.744
Nr of girls and women[a]	0.239	0.198	−0.162	0.704	1.463	1	0.226	0.139	0.434
Habitat[b]	1.801	0.898	−0.005	3.988	3.443	1	0.064	0.638	2.511

It was analyzed whether the probability that a tuber species was collected ($N = 250$; model $\mathrm{T}_{\mathrm{col}}$) or eaten ($N = 250$; model $\mathrm{T}_{\mathrm{eat}}$) was influenced by the age and gender of the children, the number of girls and women in the group, or by the habitat (forest/agriculture) of the tuber species. The estimates are shown together with the standard errors (SE), lower and upper 95% confidence interval ($\mathrm{CI}_{\mathrm{lower}}$ and $\mathrm{CI}_{\mathrm{upper}}$), likelihood ratio tests results (χ^2, df, p-value), and the minimum and maximum estimates based on the model stability analyses (min and max). Significant results ($p < 0.05$) are indicated in bold. Model $\mathrm{T}_{\mathrm{col}}$: Full-null model comparison: $\chi^2 = 12.100$, df = 4, $P = 0.017$; marginal R^2: 0.110, conditional R^2: 0.301. Model $\mathrm{T}_{\mathrm{eat}}$: Full-null model comparison: $\chi^2 = 5.052$, df = 4, $p = 0.282$; marginal R^2: 0.129, conditional R^2: 0.324. [a] Z-transformed; mean ± SD of original variables age and number of girls and women were 9.737 ± 3.321 and 3.887 ± 2.422, respectively. [b] The variables gender and habitat were dummy coded with girl and forest as reference, respectively.

prefer sweet foods (Desor and Beauchamp, 1987; Coldwell et al., 2009; Pellegrino et al., 2018), possibly explaining why fruits were eaten frequently by the children. This has also been observed in children of the Mbuti in the Democratic Republic of the Congo (Hart and Hart, 1986). The high proportion of tubers is consistent with previous studies claiming their importance for forager societies (Bahuchet et al., 1991; Dounias,

TABLE 3 Botanical knowledge of foraging-related plant species.

Term	Estimate	SE	CI$_{lower}$	CI$_{upper}$	χ^2	df	P	Min	Max
Model B$_{know}$	Botanical knowledge of foraging-related plant species								
Intercept	−2.135	0.614	−3.765	−1.030	–	–	–	−2.521	−1.608
Age[a]	**1.045**	**0.269**	**0.582**	**1.783**	**12.712**	**1**	**<0.001**	**0.907**	**1.234**
Gender[b]	0.282	0.525	−0.837	1.373	0.269	1	0.604	−0.214	0.621
Part shown	–	–	–	–	**9.885**	**4**	**0.042**	–	–
Picture fruit/ seed[b]	**2.735**	**0.883**	**0.987**	**5.020**	–	–	**0.002**	**2.417**	**3.140**
Picture trunk[b]	**1.556**	**0.573**	**0.463**	**2.980**	–	–	**0.007**	**1.224**	**1.942**
Picture leaf[b]	0.686	0.402	−0.109	1.647	–	–	0.088	0.505	0.980
Dried leaf[b]	**1.044**	**0.486**	**0.120**	**2.183**	–	–	**0.032**	**0.831**	**1.352**

The effect of age, gender, and part of the foraging-related plant species shown on the probability of correctly identifying the species was examined ($N = 1{,}020$; model B$_{know}$). Shown are the estimates together with the standard errors (SE), lower and upper 95% confidence interval (CI$_{lower}$ and CI$_{upper}$), likelihood ratio tests results (χ^2, df, p-value), as well as the statistical significance of the individual parts shown with picture bark as reference (p-value), and the minimum and maximum estimates based on the model stability analyses (min and max). Significant results ($p < 0.05$) are indicated in bold. Model B$_{know}$: Full-null model comparison: $\chi^2 = 28.284$, df = 6, $p < 0.001$; marginal R^2: 0.164, conditional R^2: 0.685. [a] Z-transformed; mean ± SD of original variable age was 11.646 ± 3.054. [b] The variables gender and those of part shown were dummy coded with girl and picture bark as reference, respectively.

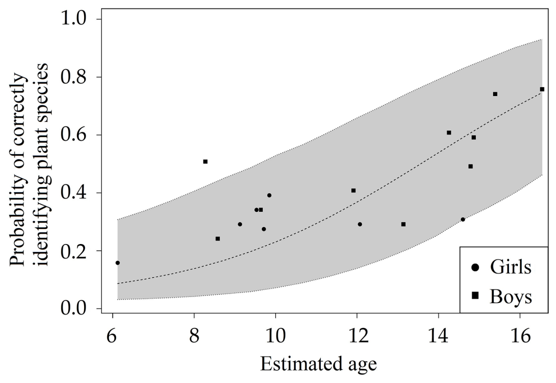

FIGURE 3
Botanical knowledge acquisition of foraging-related plant species during childhood. The relationship between age and the children's (N=17) probability to correctly answer 60 questions, in which they were asked to give the name of 12 foraging-related plant species based on pictures of different parts (i.e., fruit/seed, trunk, leaf, bark) and of the actual dried leaves. Data from girls are indicated with circles and data from boys with squares.

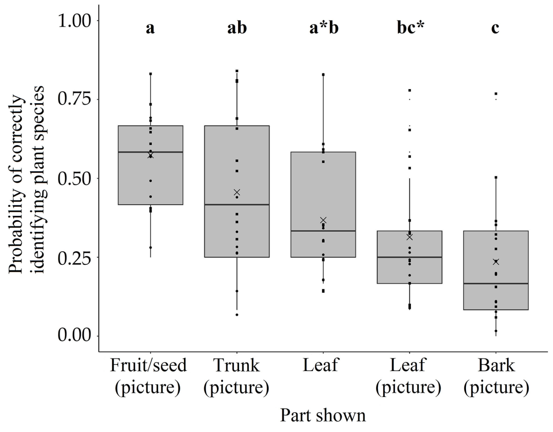

FIGURE 4
Botanical knowledge based on different plant parts. Effect of part shown on the probability of correctly identifying the plant species. Those parts with no corresponding letters indicate statistical significance (p<0.05). There was also a trend for the difference between fruit/seed (picture) and leaf and between leaf (picture) and bark (picture) (p<0.1), as indicated with an asterisk added to the letter. Data points are indicated with circles for girls and squares for boys. Finally, the mean probability per part shown is indicated with the cross.

1993; Hladik and Dounias, 1993; Kitanishi, 1995; Sato, 2001; Marlowe and Berbesque, 2009; Sato et al., 2012).

When comparing diet composition across decades, it appears that meat was substantially less eaten in our study period than two decades ago (Kitanishi, 1995). This is, however, difficult to compare directly, as Kitanishi (1995) collected within-camp data focusing on adults rather than children. Compared to adults, with the men hunting at night, children might focus more on easily collected plant foods than on game (Crittenden et al., 2013). The apparent reduced meat consumption could, on the other hand, be explained by the decreased population sizes of animal species and the increased hunting pressure coinciding with the logging activities (Yasuoka, 2006; Laporte et al., 2007). This logging activity was especially visible around camp *Bongo*. The children spent 26.9% of their time outside camp *Bongo* on logging roads, primarily searching for tubers, which appear to be in higher densities in the open areas created by the logging roads (Yasuoka, 2013). Another indication that hunting might have decreased since Kitanishi (1995) is the seemingly increased time spent eating and foraging on fish. Kelly (2013) indicated that a decreased percentage of hunting often coincides with an increased dependence on fishing in forager societies.

Finally, this study reports considerably higher percentages of agricultural foods, with 55.5% compared to 22.2% by Kitanishi (1995). In agreement with Kitanishi (1995), these agricultural foods predominantly include oil palm with 46.4% in the present study compared to their reported 50%. This increase in agricultural foods likely indicates that contemporary BaYaka have a more horticultural lifestyle than two decades ago (Kitanishi, 1995; Thompson, 2018). Such a mixed-subsistence diet might have nutritional benefits, as was indicated by improved growth in Hadza children in Tanzania (Pollom et al., 2020). However, the effect of dietary change on the nutritional status might differ between forager societies, as it often coincides with increased nutritional stress (Crittenden and Schnorr, 2017), with negative effects in !Kung foragers in Namibia (Kirchengast, 1998) and potential future health disparities between settled and foraging BaAka in Central African Republic (Remis and Jost Robinson, 2014). The nutritional effects of changing from a diet dominated by forest foods to a mixed-subsistence diet in this community is thus an important focus for future research.

Early onset gendered division in foraging activities

Children were more likely to eat fruit and seed species when there were more boys and men in the group, probably because boys and men often climb trees to collect these food types. In line with previous research on gender-segregated activities (Lew-Levy and Boyette, 2018; Lew-Levy et al., 2020a) as well as ranging patterns (Jang et al., 2019b) of BaYaka children, our results also provide evidence of the gendered division in children foraging activities. Specifically, we found that boys showed more canopy-related foraging behavior (i.e., scanning and inspecting the canopy, climbing trees) and spent more time foraging for canopy-related food items (i.e., fruits, seeds, caterpillars, honey) than did girls. Girls, in contrast, spent more time foraging for fish and digging for tubers. Especially the gendered division in honey collecting could be an interesting focus of future research, knowing its high value and potential importance later in life (e.g., as bride wealth; Lewis, 2002). However, we did not find gender differences on the probability of collecting and eating fruit and seed species. This could be explained by the way our data were collected as well as by the way these food items were shared. During fruit and seed foraging, but also with honey, often only one or a few of the boys that were strong and skilled enough climbed the trees, collected the food, and subsequently shared it with the rest of the foraging group, including the girls. Hence, the food was often not collected by the focal child and thus not considered in our data as collecting behavior, but as eating behavior by the focal child at the gathering spot. This potentially explains why the probability of eating the fruits and seeds was higher when more boys and men had been present in the foraging group.

By investigating the children's collecting and eating models in more detail, the gendered division in foraging activities became clearer, with girls being more likely to collect tuber species. The eating probability of tuber species did not, however, differ between boys and girls, potentially because forest tubers were generally processed and consumed – and thus likely shared – in camp, with 78.8% of eating time being back in camp. This is a substantially larger percentage than forest fruits, which were eaten in camp only 15.8% of the time. This low percentage stresses the importance of data collection during foraging trips, which many previous studies have not done (see Thompson, 2018). Within-camp data collection would have largely underestimated the eating time on several food items, most notably caterpillars, forest fruits, and honey (for which 66.9, 84.2, and 100% of the eating time was outside the camp, respectively).

In contrast to the forest species, the eating time on agricultural fruit and tuber species in camp was similar (81.6 and 80.4%, respectively). This high percentage of agricultural fruits eaten in camp, compared to the forest species, likely increased the eating probability by frequent food sharing in camp. Agricultural fruits might furthermore have several advantages over forest fruits. Besides the nearly year-round availability, it is expected that they are spatially more clustered with predictable locations, having oil palm, papaya, and plantain trees in the camps and gardens. They might also have some nutritional benefits (e.g., sugar-rich with low levels of fibers) over forest species (McLennan and Ganzhorn, 2017; Pollom et al., 2020). These results provide another indication that the BaYaka are in transition into a more horticultural lifestyle (Thompson, 2018).

The absence of effects of the other variables included in the model could have multiple explanations. The heterogeneity of the food species caused the instability of some of the predictors. For example, while tubers were overall more often collected by girls, species such as *Dioscorea semperflorens* are often collected by boys. In addition, "availability" can be difficult to define since the phenology of fruiting tree species varies widely (Milton, 1993; Janmaat et al., 2016) and the phenology of tubers is largely unknown (Bahuchet, 1988). Importantly, when we assumed that food items were available only 3 days before or after being foraged or eaten (models F^2_{col}, F^2_{eat}, T^2_{col}, and T^2_{eat}; Supplementary Table S9) or during the entire observation period (models F^3_{col}, F^3_{eat}, T^3_{col}, and T^3_{eat}; Supplementary Table S10), the results reported proceed to be robust.

Another potential explanation for the lack of effect of age and gender on the eating probabilities is that in an egalitarian demand-sharing society, group performance might be of greater interest than individual performance. Having no hierarchy based on age, gender, or strength (Lewis, 2014), everyone is assumed to have roughly equal probabilities of eating the food items brought back to camp by sharing. This might also explain why, contrary to our expectations, we did not find a positive effect of sweetness on eating probability. Additionally, the fruit and seed models only compared the sweetness levels within these food types, which resulted in a relatively low variation in sweetness levels. Still, the high proportion of fruits in the diet, compared to other less sweet food types, supports our expectation that children have a higher probability to eat sweet foods.

Acquisition of botanical knowledge during childhood

We found an age-related development of the botanical knowledge of foraging-related plant species in forager children. The next generation of BaYaka children might lose this plant knowledge following the transition into a more horticultural lifestyle. Such a loss in knowledge has already been demonstrated in a study comparing forest-born with town-born BaYaka (Salali et al., 2020), indicating the urgency of studies on botanical knowledge. These results suggest that childhood might enable humans to acquire the botanical knowledge needed to forage for fruits and seeds. Contrary to our predictions based on the embodied capital theory (Kaplan et al., 2000), we did not find any difference between the knowledge acquisition of girls and boys. This could be due to the limited number of older girls present in camp at the time of testing, as the difference between boys and girls likely becomes more prominent later in childhood. For the plant parts, we did find differential effects, suggesting that fruits/seeds and trunks might be especially important identifiers of foraging-related tree species. Future research should investigate the relationship between individuals' botanical knowledge and age and their foraging success rate on forest fruit and seed species.

Broader implications: The role of gender division in a developing embodied capital

Our study demonstrates a gendered division during childhood which provides insights into the development of embodied capital

(Kaplan et al., 2000). Already from an early age, the gender-specific foraging activities offer the children an opportunity to learn the foraging skills required for the collection of a wide variety of food items such as fruits and tubers.

The energetic costs of gathering should not be underestimated (Gallois and Henry, 2021), and our observed behaviors indicate that food acquisition in a rainforest is a substantial challenge with regard to both its localization and collection. Children spent substantially more time foraging for the forest tubers than for the agricultural tubers. This may be because adults prevented them from entering the garden. Yet, a more likely explanation is that agricultural tubers were in known locations (i.e., gardens) whereas forest ones might be more patchily distributed and took longer to detect (Jang et al., 2019a). Once the tuber patches were found, the BaYaka children also took longer to dig up forest tubers compared to agricultural ones, which was consistent with earlier studies that indicated that foraging on forest tubers is particularly challenging (Dounias, 1993; Sato et al., 2012). Additionally, we found clear seasonal fluctuations in foraging activities, especially of forest fruits, caterpillars, and honey. This implies that food locations or species identification skills should be remembered over long time intervals, further challenging the forager's cognition. Our results showed that their ability to identify foraging-related plant species by use of their fruit/seed and trunk of trees developed from a young age. This is exceptional knowing the tree species richness in this forest, with studies reporting as many as 72 tree species (DBH > 10 cm) for a single hectare in this research region (Loubelo Madiela, 2018).

Building on the theory of Kaplan et al. (2000), these findings clearly demonstrate the complexity involved with foraging. The activities of children include foraging for fruits and tubers, but also inspecting and climbing trees for honey or constructing dams to fish, each of which require specific skills that are developed during childhood. Investing in learning these wide variety of foraging strategies early in life possibly leads to higher productivity later in life, offering a likely explanation for our species' extreme brain size and extended childhood (Kaplan et al., 2000, 2003). Future studies should focus on the stepwise acquisition of these skills, expecting a gradual increase in complexity and productivity as they age (Kaplan et al., 2000). The youngest children might focus more on easily targeted plant foods such as agricultural fruits while later in childhood both more and more diverse foods will be foraged (e.g., honey collection). This increase in complexity in foraging skills during childhood likely coincides with a division of foraging activities. It could be especially the early onset and development of a gender-based specialization, in combination with frequent sharing of foods, that enabled the human species to obtain a more energy-rich but mainly a more stable energy supply compared to that of our closest living relatives – a supply that ultimately enabled us to afford a substantially larger brain. Such speculations could be tested in the future by more detailed investigations on gender differences in specialized foraging skills in the BaYaka and other foraging communities, but especially between different primate species, taking a comparative phylogenetic approach (Nunn, 2011). Using a similar approach, Kraft et al. (2021) found that human foragers have, compared with great apes, increased energy acquisition rates, affording the energetic costs required for our extended childhood and enlarged brains.

Our findings raise interesting questions about the evolution of skill acquisition in human development, but also inform us on how to address these in comparative studies of other extant primates. For example, seeing the trunk triggers chimpanzees to stop and look up to the crown of trees to inspect for fruits, but only for species that are in season and not for those that are out of season (Janmaat et al., 2013a). This raises the question of whether this is achieved through remembering the location of suitable trees, or whether chimpanzees are able to distinguish tree species based on characteristics of the trunk alone. We were able to distinguish these possibilities for BaYaka children by factoring out tree location using pictures. Future studies on chimpanzee's botanical knowledge could establish whether the capacity to recognize tree species using the trunk alone pre-dated humans, or evolved specifically in the context of the extended human life cycle.

BaYaka children predominantly ate a large proportion of agricultural species, which as noted above indicates that the BaYaka are in a transition into a more horticultural lifestyle. This transition does not stand on its own. Today, almost, if not all, remaining forager societies have a mixed-subsistence diet similar to the one reported here (Crittenden and Schnorr, 2017). The irreversible process of globalization and increased market integration will likely affect the children's development of their embodied capital and corresponding foraging cognition, making them perhaps one of the last generations that can inform us about the development of foraging skills. Even though these contemporary foraging societies are not an analogy of our past, they can collectively provide knowledge of our evolutionary past (Kelly, 2013). By systematically documenting the last remaining forager diets, while considering aspects such as nutritional characteristics and seasonality, inferences can be made about the subsistence behavior of foraging societies in the past. Especially the focus on the foraging contributions of children can help us answer questions about the evolutionary function of the development of skills and knowledge, and our extended childhood and its role in brain size evolution.

Overall, these results stress the importance of the forest for the BaYaka and the potentially detrimental effects the current logging activity has on their diet composition, foraging skills, and botanical knowledge. The loss of this forest will coincide with the loss of an extensive foraging cognition developed from an early age that ranges from tuber foraging skills to the knowledge of a wide number of foraging-related tree species. The change in dietary composition may have inevitable consequences for the development of these and future BaYaka forager children. Even more important than documenting this rapid process is listening to the voices of the forager people concerned.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The studies involving human participants were reviewed and approved by relevant authorities of the Republic of the Congo (Research Approval Numbers for the research on BaYaka children: N°070/MRSIT/IRSEN/DG/DS and N°378/MRSIT/IRSEN/DG/DS from the Ministère de la Recherche Scientifique et de l'Innovation Technologique) and the Comité d'Ethique de la Recherche en Sciences de la Sante (CERSSA) (N°095/MRSIT/IRSA/CERSSA). Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin.

Author contributions

JV, VK, and KJ: conceptualization. JV, HJ, BP, VK, and KJ: data collection. JV and KJ: formal analysis, investigation, and writing – original draft preparation. VK, ND, SD, PH, and AW: nutritional analyses. JV, HJ, DR, BP, PM, SD, and KJ: writing – review and editing. JV, ND, AW, and KJ: funding acquisition. PM and KJ: supervision. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

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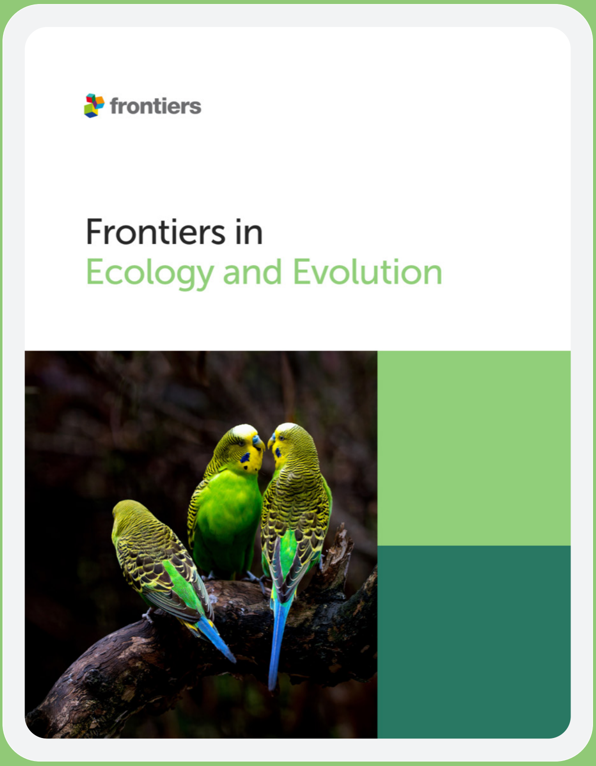

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